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Some effects of modern lighting technologies on bat activity and potential for mitigation

Some effects of modern lighting technologies on bat activity and potential for mitigation

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Abstract

Over the past two centuries, artificial light at night (ALAN) has increased globally, with rapid growth in the last 60 years due to the rise of urbanisation and industrialisation. Among the main contributors to ALAN are street lights because of their ubiquity across the world. The number of street lights is not only increasing, but their spectral signatures are also changing; currently there is a trend to use broad-spectrum lights, such as light-emitting diode (LED), metal halide (MH) and fluorescent (FL) lights. These switch-overs in technology may result in both financial and environmental improvements, but ecological impacts have not been fully considered.

I explored the ecological impacts of ALAN, by investigating the effects of street lighting on bats, which have the potential to be affected by street lights due to their predominantly nocturnal behaviour. Bats are often described as being light-opportunistic (fast-flying bats that feed on the increased number of insects attracted to the light) and light-averse (slow-flying bats that avoid lit areas probably due to the perceived risk of predation).

Switching from low-pressure sodium (LPS) to LED lights did not affect the activity or the number of feeding buzzes of those bats found in close proximity to street lights at 12 suburban sites across south Britain. From a conservation viewpoint, these results are positive as they show that LED lights are not affecting the local bats any differently from LPS lights. However, most bats recorded were light-opportunistic species, where artificial lighting seems to have less effect than for slow-flying species.

In addition to installing LED lights, many local authorities are also implementing cost-saving strategies such as dimming. Reducing the light intensity by 25% of its original output did not significantly affect the number of passes of light-averse (*Myotis* spp.) or light-opportunistic species (*Pipistrellus pipistrellus*). This is a particularly encouraging result for light-averse species, many of which are often described as threatened. It might be possible to use dimming to achieve a light intensity that reduces the ecological impact of street lighting that is acceptable for human vision and also offers cost benefits.

In addition to affecting local insect populations, the spectral emissions of street lights may also vary in relation to the spectral sensitivity of bats eyes, thereby having implications for street lighting guidelines. British bats have UV-transmissive lenses, so are sensitive to UV wavelengths that are emitted from FL and MH, but not LED, lights. The results from all three experiments, in addition to research in the current literature suggest that where street lighting is necessary, LED lights should be installed as they can be adapted to mitigate some of the negative ecological impacts of ALAN.

Dedication

For my wonderful Dad, Alan Frederick Smith

Acknowledgements

First and foremost, I would like to thank my incredible husband Neil, who has supported me in every way possible during this PhD and life in general. Without your constant encouragement, fieldwork assistance and patience I would not have got to the end of this PhD. I would also like to thank my darling children, Wilf and Maggie, who were both born during my PhD. Without knowing it, you have both helped me so much and I hope I make you guys proud. I would also like to thank my wonderful family, particularly my Mum and Dad, who have always been there for me no matter what. Sadly, my Dad passed away during my second year and did not see me complete my PhD, so this is for you Dad.

Thank you to my amazing supervisors, Gareth Jones and Stephen Harris, who have always provided sound advice and allowed me independence to conduct my research, whilst always offering continual reassurance. By being so approachable and understanding, I have felt that I could talk to you about any problem, however trivial. There are a number of people that have helped with my project, including Andy Wakefield, Ron Douglas and particularly Moth Broyles, who assisted with bat call and insect identifications in the switch-over experiment (chapter two) and Shelby Temple who provided much support, training and knowledge in the UV transmission experiment (chapter four). In the Bat Lab, special mentions to Matt Zeale, Lia Gilmour, Jérémy Froidevaux, Angelica Menchaca Rodriguez, Parvathy Venugopal and Andy Carr who have provided great moral support throughout my PhD journey.

Thank you to all the councils and contractors that assisted with the project, particularly Bath and North East Somerset Council, Berkshire Council, East Sussex Council, Gloucestershire County Council, Hertfordshire County Council, Ringway, South Gloucestershire Council and Telensa who provided all the logistical help that made this study possible. I would particularly like to thank Hertfordshire County Council and Jon Watt and Graham Black from Ringway and Trevor Byrne from Telensa for their incredible support and assistance in the dimming experiment (chapter three).

Finally I would like to thank the Natural Environment Research Council (NERC) for funding my project.

Author’s Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

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Abbreviations and acronyms

β	Secondary absorption peak
λ	Wavelength (nm)
λ_{max}	Wavelength of maximum absorption
AIC	Akaike's Information Criterion
AICc	Second order information criterion
ALAN	Artificial light at night
BACI	Before-after-control-impact
CCT	Correlated Colour Temperature
CF	Constant frequency
CMS	Central management system
CH_4	Methane
CI	Confidence Interval
CO_2	Carbon dioxide
Column	Lamp-post
CRI	Colour Rendering Index
dB	Decibels
df	Degrees of freedom
EU	European Union
FL	FL
FM	Frequency modulated
GLMM	Generalized Linear Mixed Models
HDC	High-duty cycle
HPMV	High-pressure mercury vapour
HPS	High-pressure sodium
IR	Infrared
K	Kelvin
LDC	Low-duty cycle
LE	Luminous efficacy
LEDC	Cool-white LED
LED(s)	Light-emitting diode(s)
LEDW	Warm-white LED
Lm	Lumens
LPS	Low-pressure sodium
LWS	Long-wavelength-sensitive
lx	Lux
MH	MH
MWS	Medium-wavelength-sensitive
M/LWS	Medium-to-long wavelength
n	Sample size
nm	Nanometres
PNL	Part-night lighting
PWM	Pulse-width modulation
R^2	Coefficient of determination
RH	Rhodopsin
SD	Standard Deviation
SE	Standard Error
sr	Steradian
SSL	Solid state lighting

SWS	Short-wavelength sensitive
T	Standard score / z-value
T_{50}	Wavelength (nm) that is 50% of the maximal transmittance
Tg	Teragram
UK	United Kingdom
µm	Micrometres
UV	Ultra-violet
UVA	Ultra-violet A
UVB	Ultra-violet B
UVC	Ultra-violet C
vs.	Versus
W	Watts
WAV	Waveform audio file
z	Standard score / z-value

Publications and collaborators contributions

Chapter one forms the basis of a book chapter, with considerable re-writing and updating to include recent research from the literature. Chapters two and three form the basis of independent papers and all include a degree of overlap and repetition. I am hoping to submit chapter four as soon as possible. Here, I acknowledge the contributions for each paper.

Chapter 1: Rowse, E.G., Lewanzik, D., Stone, E.L., Harris, S. & Jones, G. (2016). Dark Matters: The Effects of Artificial Lighting on Bats. In: C. C. Voigt & T. Kingston (Eds). *Bats in the Anthropocene: Conservation of Bats in a Changing World* (pp. 187-207). USA: Springer Open. The only material included in this section of the thesis is what I wrote in the book chapter, most of which has been substantially updated since publication to include literature recently published (Appendix I).

Chapter 2: Rowse, E.G., Harris, S. & Jones, G. (2016). The Switch from Low-Pressure Sodium to Light Emitting Diodes Does Not Affect Bat Activity at Street Lights. *PLoS One*, **11**(3), e0150884. doi:10.1371/journal.pone.0150884. E.G.R. co-designed the experiment, collected and analysed data and drafted the manuscript. G.J. and S.H. were involved in securing funding, study design and co-ordination and edited the manuscript. Moths Broyles identified insects and bat calls around High-pressure sodium street lights, neither of these data were used in the above paper, but the results are presented in the thesis (Appendix II).

Chapter 3: Rowse, E.G., Harris, S. & Jones, G. (2018). Effects of dimming light-emitting diode street lights on light-opportunistic and light-averse bats in suburban habitats. *Royal Society Open Science*, **5**, 180205. doi: 10.1098/rsos.180205. E.G.R. co-designed the experiment, collected and analysed data and drafted the manuscript. G.J. and S.H. were involved in securing funding, study design and co-ordination and edited the manuscript. (Appendix III).

Chapter 4: Rowse, E. G., Harris, S., Jones, G. & Temple, S. (**to be submitted**). The spectral transmission of light through the lenses of bat eyes: implications for modern street lighting. E.G.R. co-designed the experiment, collected and analysed data and

drafted the manuscript. S.T. was involved in study design and edited the manuscript. G.J. and S.H. were involved in securing funding and edited the manuscript.

Chapter 1: Introduction

Part of this chapter has been published in:

Rowse, E. G., Lewanzik, D., Stone, E. L., Harris, S. & Jones, G. (2015). Dark Matters: The Effects of artificial lighting on bats. In C. C Voigt & T. Kingston (Eds.), *Bats in the Anthropocene: Conservation of bats in a changing world* (pp. 187-207).USA: Springer Open (Appendix I).

1.1. Anthropogenic pollution

Anthropogenic pollution is pervasive and as a result has major impacts on our environment, biodiversity and even human health. Although, anatomically modern humans have been around for ~ 200,000 years (McDougall *et al.* 2005), our impact on earth does not seem evident until the start of the Holocene (~ 12,000 years ago) with the beginning of the Neolithic agricultural revolution (Ruddiman *et al.* 2015). Since then, human-driven changes have showed no signs of slowing down and this is mainly due to rapid growth of the human population, increased use of resources and technological advancements (Waters *et al.* 2016). Over time humans have completely re-engineered the Earth's landscape by removing large forested and grassland areas for agricultural uses, creating built environments and manufacturing natural resources (Ruddiman *et al.* 2015). Industrialisation and urbanisation have only further exacerbated these changes (Waters *et al.* 2016). Global changes in atmospheric greenhouse gases, most notably carbon dioxide (CO_2) and methane (CH_4) have resulted in climate change (Ruddiman *et al.* 2015). These atmospheric gases have been increasing since the intensification of agricultural practices, with a marked rise in the industrial revolution (~ 1850), an upward trajectory that continues today (Ruddiman *et al.* 2015; Waters *et al.* 2016). Climate change in addition to habitat loss, overexploitation and invasive species have become key drivers in biodiversity loss, which could disrupt ecosystem functions and services, such as pollination, pest control and human health (Sala *et al.* 2000; Hoffmann *et al.* 2010; Dirzo *et al.* 2014).

As well as disrupting natural systems, many human activities also release new anthropogenic materials onto the Earth's surface. Plastics, for example have a biomass (~ 300Tg) that is akin to the human biomass (Waters *et al.* 2016). General use for plastics has increased in popularity since their commercial development in the 1930s and 1940s (Jambeck *et al.* 2015). However, because plastics are so durable and can persist for long periods of time, they are a significant environmental threat (Ryan *et al.* 2009). The disproportionate impact that humans are having on the Earth's environment, has caused many scientists to believe that we have entered a new geological epoch, the Anthropocene (Crutzen & Stoermer 2000; Ruddiman *et al.* 2015), which is viewed as the period during which human activity has been the dominant influence on climate and the environment. The start date of the Anthropocene is widely debated, although most scientists agree it occurred somewhere between the late 18th Century and mid-20th century (Ruddiman *et al.* 2015). While some organisms can adapt to human-altered environments, many cannot and are currently undergoing population declines (Cardillo *et al.* 2008). As defaunation contributes to a major loss of biodiversity, it is predicted to have major effects on ecosystem functions and services (Dirzo *et al.* 2014).

In addition to the direct effects of human activity, such as urbanisation and agriculture, there are a number of associated indirect effects, notably light (Hölker *et al.* 2010a), noise (Arroyo-Solís *et al.* 2013) and chemical pollution (Rhind 2009), all of which are pervasive pollutants (Grimm *et al.* 2008). Until recently, light pollution has received less attention than other anthropogenic threats, even though it can have far-reaching effects on terrestrial and marine taxa. Light pollution is comparable to plastic pollution as it is difficult to remove once present in the Earth's system and its effects can persist for long periods of time. During my thesis I will focus on the ecological impacts of light pollution (Koen *et al.* 2018).

1.2. What is light?

Before exploring the effects of light pollution, it is important to define light. The electromagnetic spectrum encompasses radiation with wavelengths ranging from less than a nanometre (gamma rays) to a kilometre (radio waves) (Campbell 2011).

When referring to light, we often focus on the wavelengths perceived by humans, known as visible light, which includes wavelengths between 400 and 700 nm (Purves & Lotto 2003) (Figure 1.1). However, many animals detect light in the ultraviolet (UV) (10-400 nm) (Douglas & Jeffery 2014) and infra-red ranges (700-1000 nm) (Schmitz & Bleckmann 1998; Land & Nilsson 2012).

Light can be described both in terms of massless particles called photons and waves with changing electric and magnetic fields (Johnsen 2012). When light interacts with objects, it can be reflected, absorbed, transmitted and/or scattered (Land & Nilsson 2012). Light can be measured according to the photometric system, which is based on human spectral sensitivities (Johnsen 2012), and the radiometric system that considers all wavelengths, not just those visible by humans (Land & Nilsson 2012). Irrespective of light being referred to in terms of particles or waves, light can only have three properties: intensity, wavelength/frequency and polarization (Cronin *et al.* 2014). In my thesis I will focus on two properties of light, intensity and wavelength/frequency. Wavelength (λ) refers to the distance between the peaks of each wave and frequency refers to the number of waves in a cycle (Hz). Wavelength and frequency have an inverse relationship, i.e. shorter wavelengths have higher frequencies and *vice versa* (Cronin *et al.* 2014).

Intensity refers to the strength or the brightness of the light and can be defined in several ways. When referring to the intensity of light, it is important to distinguish between a surface emitting light (radiance/luminance) and a surface receiving light (irradiance/illuminance). Table 1.1 summarises the common ways in which light intensity is measured. In ecology the intensity of light is generally measured as illuminance (lux). Lux is appropriate when discussing human vision as it is adjusted for human spectral sensitivities. However, as lux does not include spectral sensitivity information for a range of nocturnal taxa, it is of limited benefit to these organisms. Nevertheless, to ensure interdisciplinary collaboration, it is necessary to follow a system that can be adopted by all stakeholders, i.e. biologists, lighting engineers, designers, etc.

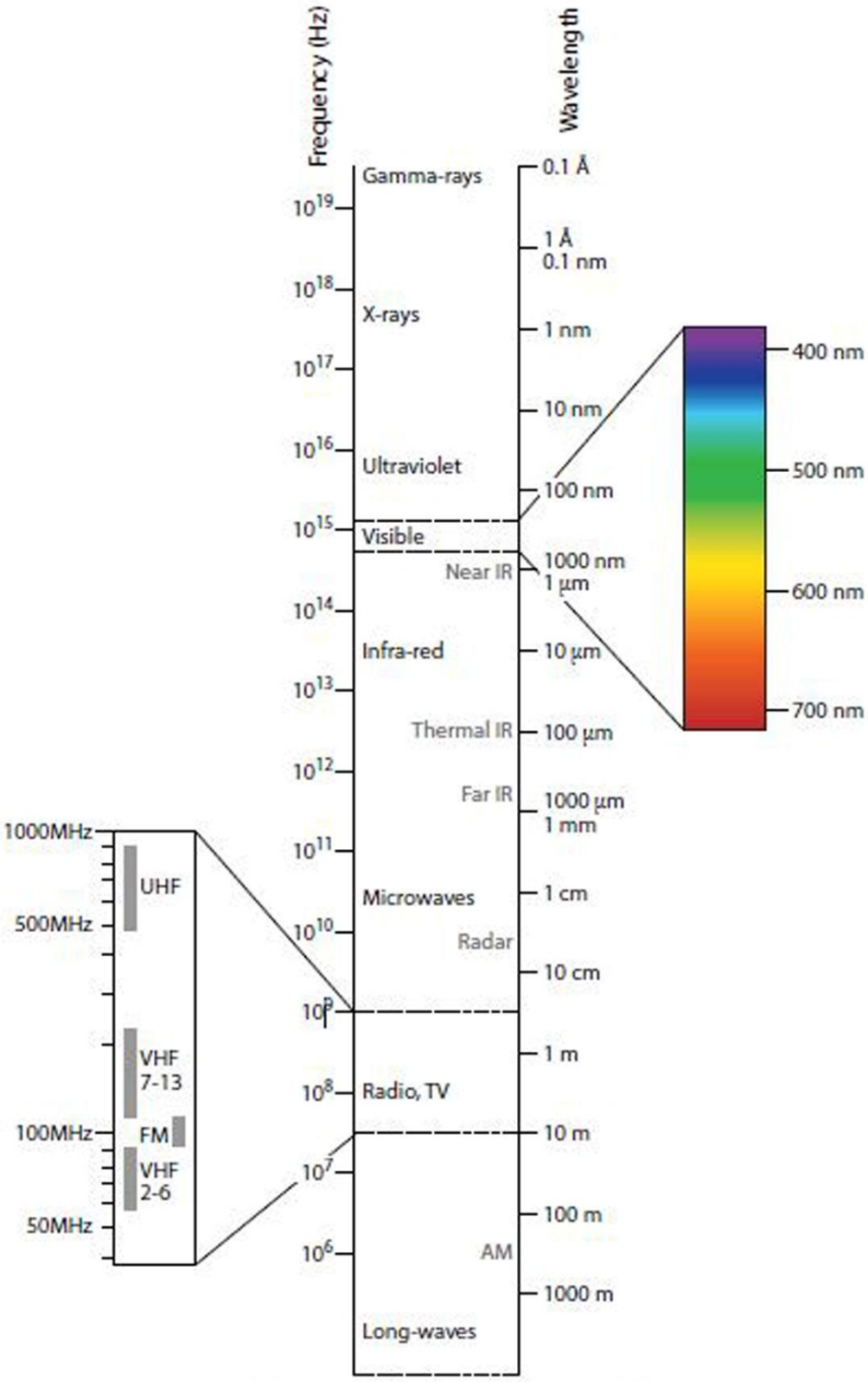

Figure 1.1. The electromagnetic spectrum, where the “visible” spectrum means visible to humans. Taken from Cronin *et al.* (2014).

Table 1.1. Common lighting terms and their definitions

Lighting term	Radiometric/photometric	Unit	Definition
Illuminance	Photometric	Lux (lx)	Luminous flux per unit area of a surface adjusted for human spectral sensitivity
Irradiance	Radiometric	photons.s^{-1} m^{-2} nm^{-1} or watts.s^{-1} m^{-2} nm^{-1}	Radiant flux per unit area of a surface for each wavelength
Luminance	Photometric	Candela per square metre (Cd/m^2)	Luminous intensity emitted per unit area of a surface in a specific direction adjusted for human spectral sensitivity
Luminous efficacy	Photometric	Lumens/W	Ratio of luminous flux and power and specifies the efficiency of the light source
Luminous flux	Photometric	Lumens (lm)	The amount of light emitted by a light source but does not specify the direction in which the light is radiating
Luminous intensity	Photometric	Candela (Cd)	Luminous flux emitted in a specified direction
Radiance	Radiometric	photons.s^{-1} $m^{-2}sr^{-1}nm^{-1}$ or watts.s^{-1} $m^{-2}sr^{-1}nm^{-1}$	Radiant intensity emitted per unit area per steradian (a conical sector of a sphere) per wavelength

1.3. Vision

The ability to perceive light allows organisms to interact with their environment. Eyes range from single cells to complex organs such as compound eyes. Many insects have compound eyes that are made up of many light detectors called ommatidia, each of which contains its own lens. A compound eye is beneficial for insects as it allows them to detect movement, which is important when evading predators. All vertebrates and many invertebrates have single lens eyes. The light enters the eye through the pupil and is then focussed on the retina by the lens. Light is detected by photoreceptor cells within the retina known as rods and cones (Land & Nilsson 2012). Rods are more sensitive to light than cones but cannot detect colour. Rods enable vision during the night (scotopic vision, for luminances under ~0.01 cd/m^2), whereas cones are involved in colour vision and sensitive to bright light, such as in the day (photopic vision, for luminances over ~3 cd/m^2). During low light levels, such as dusk and dawn, both rods and cones work together (mesopic vision) (Müller, Goodman & Peichl 2007).

Cones and rods contain light-absorbing pigments known as visual pigments (opsin and chromophore). The sensitivity of these visual pigments determine the wavelength perceived by the photoreceptor cell, which depends on the maximal spectral absorption (λ_{max}) of the visual pigment (Khokhlova 2012). Colour vision requires an animal to possess at least two colour visual pigments that have different λ_{max} values (Bowmaker 2008). It is not possible to distinguish between wavelength and intensity when only one colour visual pigment is present, and so the organism has monochromatic vision (Land & Nilsson 2012).

Five classes of opsin pigments are found in vertebrates: long-wavelength sensitive (LWS) 495-570 nm (red/green), medium-wavelength sensitive (MWS) 470-530 nm (green), short-wavelength sensitive (SWS2) 415-480 nm, SWS1 355-450 nm (UV/violet) and rod pigment (rhodopsin) (RH1) 460-530nm (blue-green). Most mammals are dichromats, i.e. contain two cone opsins, typically SWS1 and either MWS or LWS, as well as the rod pigment RH1. However, many invertebrates tend to have trichromatic vision (three cone opsins) or even tetrachromatic vision (four cone opsins) (Land & Nilsson 2012). Birds are typically tetrachromats, with a SWS1, a SWS2, a MWS and a LWS visual pigment (Lind *et al.* 2013).

1.4. Growth of ALAN

There was a transformation of the night skies during the 20th century. A dramatic increase in artificial lighting at night (ALAN) means that celestial bodies, such as the moon and stars, are no longer the only night-time light sources. Artificial lighting has increased because of urbanisation, population growth, economic development and advances in lighting technologies, and provides numerous economic, commercial, recreational and security benefits (Riegel 1973; Hölker *et al.* 2010a; Davies, Bennie & Gaston 2012).

Improvements in technology, particularly the use of satellites with calibrated radiometers, mean that it is now possible to obtain high resolution measures of ALAN at a global scale (Falchi *et al.* 2016; Kyba *et al.* 2017). These reveal major trends: from 2012 to 2016, ALAN in lit areas grew by 2.2% per year, and in all areas by 1.8% (Kyba *et al.* 2017). Approximately 83% of the world's population lives under skies polluted by ALAN (Falchi *et al.* 2016). However, the satellites used to produce these data are only sensitive to the 500-900 nm range, which excludes the blue and violet part of the visible spectrum (Falchi *et al.* 2016). So, these satellites cannot quantify all emissions equally, and omit the shorter wavelengths included in the spectra of modern lighting types such as lighting emitting diodes (LED), the use of which has increased over the last decade.

ALAN includes astronomical light pollution, the light that disrupts viewing of stars and other celestial matter, and ecological light pollution, which has direct ecological effects (Longcore & Rich 2004). I focus on ecological light pollution, which can be caused by glare (extreme contrasts between bright and dark areas), over-illumination, light clutter (unnecessary numbers of light sources), light trespass (unwanted light) and skyglow, where artificial light is directed towards the sky, scattered by atmospheric molecules and reflected back to earth (Royal Commission on Environmental Pollution 2009; Gaston *et al.* 2012; Kyba & Hölker 2013).

Light pollution is now considered a global threat and, while it is currently more apparent in developed nations (Figure 1.2), projected increases in industrial and urban growth suggest that light pollution will also increase in developing countries (Cinzano, Falchi & Elvidge 2001; Hölker *et al.* 2010b; Gaston *et al.* 2012; Bennie *et*

al. 2014). ALAN is a significant threat because of its far-reaching effects; the impacts of light pollution on pristine environments such as national parks can be the caused by light sources hundreds of kilometres away (Kyba *et al.* 2017).

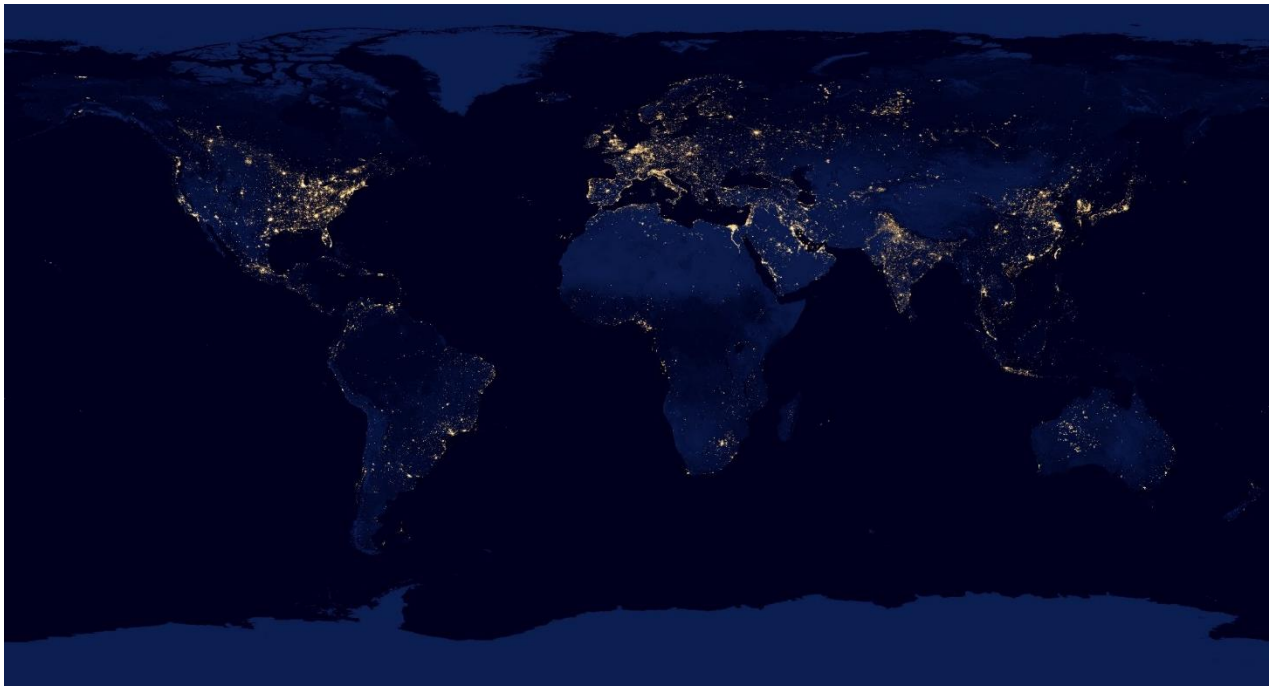

Figure 1.2. Artificial lighting is currently most widespread in the developed world. Global use of lighting at night in 2000. From NASA Earth Observatory/NOAA NGDC (2012).

1.5. Types of artificial light

Artificial lighting has infiltrated all aspects of human life both indoors and outside, including buildings, advertisements, security and vehicular lights (Gaston *et al.* 2012; Kyba *et al.* 2015). In this thesis I focus on street lighting because of its universal use and potential for ecological impacts (Gaston *et al.* 2012). This contribution to ALAN is particularly important because street lighting consumes between 60% and 80% of electricity per municipality (Fiaschi *et al.* 2012).

1.6. History of street lights

Street lights have a range of spectral signatures (Figure 1.3); their primary emissions depend on the type of reactive material and/or coating in the lamps (Buchanan 2006).

There have been three main technological changes in street lighting: the use of incandescent, gas discharge and solid-state lamps (De Almeida *et al.* 2014). Incandescent lamps, developed by Thomas Edison in 1880, emit long wavelengths with a maximum intensity between 900 and 1050 nm (Elvidge *et al.* 2010). Despite improvements such as the quartz halogen lamp, which uses an inert gas to preserve the tungsten filament, incandescent lamps are still relatively inefficient because their emissions are predominantly near the infrared spectrum (~80%) and so largely invisible to humans (Elvidge *et al.* 2010). They only convert 4-5 % of the electricity consumed into usable light (De Almeida *et al.* 2014).

By the mid-twentieth century, gas discharge lamps were developed that produced light by passing electric arcs through gas-filled bulbs (Elvidge *et al.* 2010). These are more energy efficient than incandescent lamps as they emit the majority of their wavelengths within the human spectral range (Elvidge *et al.* 2010). Gas discharge lamps include low-pressure sodium (LPS), which has a narrow spectral signature, emitting an almost monochromatic orange light with a peak intensity of 589 nm (Figure 1.3) (Rydell 2006; Elvidge *et al.* 2010). High pressure sodium (HPS) lamps, which emit yellow-orange light and a range of “white” lamps, include fluorescent (FL), high-pressure mercury vapour (HPMV) and metal halide (MH) lamps. Gas discharge lamps replaced incandescent lamps because of their energy efficiency and improved longevity (Schubert & Kim 2005), and LPS (44%) and HPS (41%) lamps came to dominate street lighting in the UK (Royal Commission on Environmental Pollution 2009) and elsewhere. The luminous efficacy (LE) (amount of light produced per watt of electricity) of gas discharge lamps is five times higher than for incandescent lamps (Schubert & Kim 2005; Elvidge *et al.* 2010).

The broad spectrum “white” discharge lamps emit some UV wavelengths (Rydell 2006; Elvidge *et al.* 2010). In 2010 HPMV lamps contributed 80% of the global

lighting market (Baumgartner *et al.* 2012). However, since 2015, HPMV lights are no longer being installed in Europe because they do not meet minimum performance and efficiency standards (EU 2009), although MH and FL lamps are still used in street lights due to their increased colour rendering index (CRI) (Williams 2009; Stone *et al.* 2015).

The CRI compares how accurately a light source replicates the full range of colours of an object viewed in natural light on a scale of 0-100, where 100 is equivalent to natural light (Schubert & Kim 2005; Elvidge *et al.* 2010; Davies *et al.* 2013). HPS lamps typically have a CRI between 7 and 32, whereas MH lamps have a CRI ranging from 64 to 100, reflecting their ability to render colour more suited for human vision (Elvidge *et al.* 2010; Gaston *et al.* 2012). Since street lights exist primarily for perceived safety benefits, improved colour rendering for human vision enables people to see their surroundings more clearly, making them feel less vulnerable at night (Lyytimäki *et al.* 2008).

However, with pressure to reduce energy use and CO_2 emissions, the lighting industry is now using solid-state lighting (SSL) technologies such as LED lights (Elvidge *et al.* 2010; Gaston *et al.* 2012). LEDs are very energy efficient because they convert all the electricity into light by the movement of electrons across a semiconductor (De Almeida *et al.* 2014) and have broad spectral signatures, typically 400–700 nm, with virtually no emissions in the UV range (Elvidge *et al.* 2010). Originally this was achieved using cerium-doped yttrium aluminium garnet (YAG:Ce) phosphors with a gallium nitride (GaN), which converts monochromatic blue to “white” light. More recently, LED lights can produce light by combining multiple monochromatic sources (red, green and blue), which allows for greater control over spectral emissions (Narendran *et al.* 2004; Gaston *et al.* 2012, 2013; Davies *et al.* 2013). LED lamps have a number of advantages over their gas-discharge counterparts, including: high CRI (65-100) (Elvidge *et al.* 2010); low running costs (Gaston *et al.* 2012); low energy consumption (Elvidge *et al.* 2010); controllability of spectral, temporal and intensity of emissions; reduced CO_2 emissions (Hölker *et al.* 2010a); and smart lighting capabilities that enable dimming in response to weather, traffic and lunar conditions (Bennie *et al.* 2014).

There are three major types of LED lights, cool, neutral and warm, that vary according to their correlated colour temperature (CCT), which is measured in Kelvins. Cool LEDs appear “cold” and have a high colour temperature (~6000 K), warm LEDs have a “warmer” appearance (~2700 K), and neutral LED lights have a colour temperature between cool and warm LED lights (~4000 K) (Longcore *et al.* 2015).

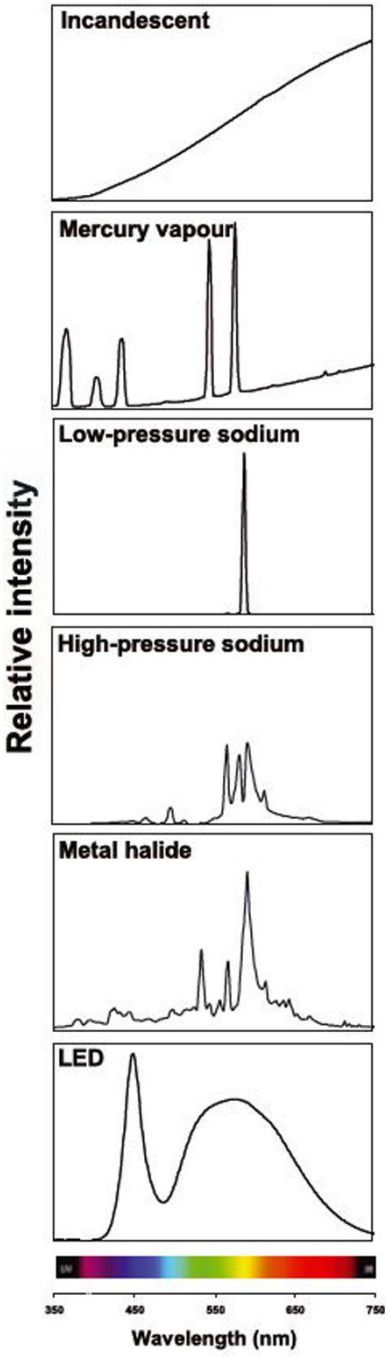

Figure 1.3. The spectral composition of common lighting technologies. From Gaston et al. (2013).

1.7. Projected changes in street lighting

LED lights are already being used in a range of outdoor applications, including vehicular lighting, signal lighting and traffic lights, and their use is predicted to increase (De Almeida *et al.* 2014). According to Haitz's law, the cost per lumen reduces by a factor of 10 every decade and the amount of light generated per LED increases by a factor of 20 for any given wavelength (De Almeida *et al.* 2014). This could lead to a phenomenon known as the "rebound effect", where cheaper prices result in a rise in the use of LED lights for existing, as well as new applications. Such an increase in the use of LED lights would nullify many of the potential environmental advantages, such as increased energy efficiency and reduced greenhouse gas emissions (Jenkins *et al.* 2011).

International lighting policies are prioritising energy-efficient technologies to reduce costs and CO_2 emissions. The European Ecodesign Directive 2009/125/EC, for instance, encourages switching from energy-intensive technologies such as incandescent, LPS, HPS and HPMV lamps (Hölker *et al.* 2010a) to "whiter" lighting with higher colour rendering capabilities, increased energy efficiency and flexibility (Gaston *et al.* 2012; Jagerbrand 2016). Although LED lights are the preferred choice, FL and MH street lights are still used due to the reduced cost (Williams 2009; Stone *et al.* 2015). The switch-over to broad-spectrum light sources may reduce CO_2 emissions in the EU by as much as 42 Mt per year. A number of pilot studies in cities around the world (including Adelaide, Hong Kong, London, Mumbai, New York, Sydney and Toronto) have compared LED lamps against existing lighting technologies. After a three-year trial, the City of Sydney Council agreed to switch to LEDs on 6500 outdoor lights due to their reduced energy consumption, cost-effectiveness and improved illuminance (The Climate Group 2014).

Future research will focus on increasing the efficiencies of LED lights by developing internal quantum efficiency (the ratio between electrons and photons across the semiconductor material), the extraction efficiency (the process of extracting photons from the semiconductor material) and scattering efficiency (extracting photons from the phosphor). By 2020, it is predicted that both cool and warm LED lights will have a LE of approximately 250 lm/W (De Almeida *et al.* 2014).

1.8. Ecological effects of ALAN

The effects of ALAN are widespread and affect a range of organisms, including birds, vegetation, fish, amphibians and mammals (Gaston *et al.* 2013). The increase of ALAN into unlit areas is likely to affect 30% of vertebrates and 60% of invertebrates that are nocturnal (Hölker *et al.* 2010b). This is unsurprising given that most of these species have evolved under a day/night cycle that is enhanced for each of its circadian rhythms (Botha *et al.* 2017). Disrupting an organism's circadian rhythm could significantly affect regulation of the sleep-wake cycle, core body temperature, metabolism, gene expression and hormone production (Stevens & Zhu 2015). A field experiment on the nocturnal grey mouse lemur (*Microcebus murinus*) showed that individuals exposed to a yellow LED light (51.5 lux) had significant changes in core temperatures, locomotor activity and oestrus cycle compared to individuals exposed to moonlight (0.3 lux) (Le Tallec *et al.* 2016). A long-term study on free-living nocturnal wallabies (*Macropus eugenii*) exposed to various light levels demonstrated that ALAN significantly reduced pineal hormone melatonin (MLT), which is important in controlling circadian rhythms and delayed reproductive activation (Robert *et al.* 2015). A number of studies on birds have shown the deleterious effects of ALAN on sleep behaviour (Sun *et al.* 2017; Raap, Pinxten & Eens 2018), immune responses (Raap *et al.* 2016) and stress hormone concentrations (Ouyang *et al.* 2015). Circadian systems are regulated by intrinsically photoreceptive retinal ganglion cells (ipRCGs) that contain melanopsin, a photopigment with a peak sensitivity (λ_{max}) around 480nm (Stevens & Zhu 2015). These internal processes can be disrupted by the reduced levels of darkness, as well as change in the spectral composition and intensities of surrounding lighting levels (Gaston *et al.* 2017). Artificial lights can have such dramatic impacts on fauna and flora because illuminance levels can be as high as 100 lux in urban areas, whereas lighting intensity from the moon is only 0.001 – 0.1 lux (Botha *et al.* 2017).

As well as internal physiological responses, ALAN can have a number of effects on key daily events. For instance, ALAN can influence the foraging behaviour of birds such as great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) by causing them to start foraging earlier (Clewley *et al.* 2016; Da Silva *et al.* 2017). ALAN can also affect the foraging behaviour of other taxa: for example, the presence of artificial

lights increased the number of large-bodied predators and small shoaling fish in an estuary in South Africa (Becker *et al.* 2013). Beach mice (*Peromyscus polionotus leucocephalus*) avoided foraging and harvesting seeds in areas that were lit with artificial light (Bird *et al.* 2004). A number of studies have also explored the effects of ALAN on migration in birds (La Sorte *et al.* 2017; van Doren *et al.* 2017; Mclaren *et al.* 2018), as well as amphibians such as the common toad (*Bufo bufo*) (van Grunsven *et al.* 2017). Satellite data showed that budburst of four deciduous tree species occurs 7.5 days earlier in artificially lit areas (Ffrench-Constant *et al.* 2016).

1.9. Effects of ALAN on insects

It is important to consider the effects of ALAN on insects as this underpins the behaviour of many bat species around artificial lighting. The effect of ALAN, particularly street lighting on insects, has long been of interest to ecologists (Bowden 1982; Frank 1988; Rydell 1992). Insects around street lights exhibit flight-to-light, or positive phototactic, behaviour, during which they are distracted from activities such as foraging. This could lead to death by coming into direct contact with the hot lantern, or through exhaustion by continually circling around the light source or through predation. Over time, this can lead to a “vacuum effect”, potentially resulting in local population declines. The distances over which insects are attracted to individual light sources will also depend on the background light levels, including skyglow and the lunar cycle. For example, during the full moon, insects will not be attracted from so far away (Eisenbeis 2006).

Spectral composition i.e. the range of wavelengths that the light emits, and the intensity of a street light will affect the positive phototactic behaviour exhibited by insects (Barrett *et al.* 1973, 1974; Frank 1988; van Grunsven *et al.* 2014; Poiani *et al.* 2015). Short wavelengths, particularly those in the UV range, are attractive to many insects because they correspond with the λ_{max} of their visual pigments in their eyes (Muirhead-Thomson 1991; Eisenbeis 2006; Cowan & Gries 2009). This means that street lights that contain UV wavelengths, for example HPMV and MH, tend to be highly attractive to insects (Eisenbeis 2006; Wakefield *et al.* 2017).

ALAN can make some insects more susceptible to nocturnal predators by interfering with complex predator-prey relationships (Minnaar *et al.* 2015). Some nocturnal moth species contain tympanate organs that are sensitive to the echolocation calls of some bat species, allowing them to often evade capture (Svensson & Rydell 1998; Minnaar *et al.* 2015). By setting up a HPMV street light and mimicking the calls of two aerial-hawking bats, the northern bat (*Eptesicus nilssoni*) and the parti-coloured bat (*Vespertilio murinus*) using an electronic dog whistle, significantly fewer moths demonstrated evasive behaviours (Svensson & Rydell 1998). This experiment was repeated using bats (*N. capensis*) instead of echolocation imitations. Again, moth consumption under lit conditions was significantly higher than under unlit conditions (Minnaar *et al.* 2015). A similar study using LED instead of HPMV lights also indicated that moths significantly reduce their evasive manoeuvres under lit, compared to unlit, sites (Wakefield *et al.* 2015). It seems that bats will be more successful at preying on tympanic moths around street lights because there are higher numbers to exploit, but also they perform fewer evasive behaviours (Svensson & Rydell 1998).

However, the biological consequences of reduced evasive behaviour by tympanate moths may not be apparent when considering bat species at the community level. A study in Missouri, USA evaluating faecal samples of six bat species showed that there was no significant difference in the number of Lepidoptera (or Diptera and Coleoptera) between lit and unlit sites. In particular, there was no increase in the number of tympanic moths consumed by bats in the lit sites compared to the unlit sites (Cravens *et al.* 2018). However, bats may have spent considerable time foraging at sites other than the ones they were captured at i.e. bats captured at lit sites may have already foraged for substantial amounts of time in unlit areas.

Studies exploring the effects of ALAN on insects are moving away from focussing on a single species to investigating community level effects (Knop *et al.* 2017). A study in Switzerland showed that there were 62% fewer visitations by nocturnal pollinators at lit plant sites compared to unlit sites. This in turn led to reduced plant reproductive success that could not be counteracted by diurnal pollinators. This potential link between diurnal and nocturnal pollinators demonstrates how ALAN can have damaging effects at a community level, as well as on individual species (Knop *et al.* 2017).

1.10. Effects of ALAN on bats

Bats belong to the order Chiroptera, which is further classified into two sub-orders Yinpterochiroptera and Yangochiroptera: the latter contains 20 families, with the Vespertilionidae being the largest (Lei & Dong 2016). Bats inhabit every continent, apart from Antarctica, but they are most diverse in the tropics and subtropics. Bats range in size from 2 g to 1.5 kg with wing spans ranging from 12 cm to 2 m (Fenton & Ratcliffe 2010). Bats have a varied diet, including insects, fruits, nectar, fish, meat and blood (Voigt & Kingston 2015), but the majority of species are insectivores (Fenton & Ratcliffe 2010).

The majority of bats are social animals, occupying roosts during the day, with numbers of bats sometimes reaching into the thousands, even millions. Bats roost in a range of habitats including rock crevices, caves, tree hollows, buildings and bridges (Fenton & Ratcliffe 2010). Although many bats are small, they have relatively long lifespans (even exceeding forty years) and slow reproductive rates (typically one pup per year), making them susceptible to population crashes (Fenton & Ratcliffe 2010). Bats are nocturnal, and this is most likely to reduce the risk of predation by diurnal birds of prey that may be difficult to detect (Rydell & Speakman 1995; Speakman *et al.* 2000).

Bats use echolocation (apart from the majority of bats in the family Pteropodidae) to build an acoustic image of their environment and detect, localise and even classify prey (Griffin 1944, 1958; Fenton, Faure & Ratcliffe 2012). Most bats produce a series of echolocation pulses using their larynx, although a few pteropodids use tongue clicks (Griffin 1958; Yovel *et al.* 2010). Typical bat echolocation calls include search phase (orienting the landscape), social calls and feeding buzzes (transition from the search phase to the approach and terminal phases of hunting). During a feeding buzz the pulse duration decreases and the pulse repetition rate and duty cycle increases (Griffin, Webster & Michael 1960; Simmons, Fenton & O'Farrell 1979; Kalko *et al.* 1998).

There are two broad types of echolocation in bats; low-duty cycle (LDC) and high-duty cycle (HDC). The duty cycle refers to the ratio of sound to silence and corresponds to signalling effort (Fenton, Faure & Ratcliffe 2012). The majority of bat

species are LDC echolocators; they will emit a call and wait for the receiving echo before emitting another call (Holderied & von Helversen 2003; Holderied *et al.* 2005). Calls from LDC echolocators are typically short in duration (1-20 ms), broadband (frequency modulated (FM)) (though sometimes narrowband) and are separated by relatively long periods of silence (signal duration is <25% of call periods during search phase of echolocation) (Fenton, Faure & Ratcliffe 2012). Bats from the families Hipposideridae and Rhinolophidae (and *Pteronotus parnellii* in the family Mormoopidae) are HDC echolocators that utilise changes in frequency rather than time, allowing them to emit and receive calls simultaneously. This highly specialised echolocation system involves call-to-call changes in frequency to compensate for Doppler shifts induced by changes in their flight speed (Schnitzler 1968; Schuller 1974, 1977). Calls emitted by HDC echolocators consist of a long constant frequency (CF) component, followed (and sometimes initiated by) by a FM component (Henson *et al.* 1987; Jones & Rayner 1989). The calls are typically long in duration (10 to >50 ms) and are separated by shorter periods of silence compared to LDC echolocators (signal duration is ≥25% of call periods during search phase of echolocation) (Fenton, Faure & Ratcliffe 2012).

The type of echolocation calls that a bat emits and its wing morphology are indicators of the habitat it uses and the type of prey it hunts. Bat wings vary according to their aspect ratio (the ratio of wingspan squared to the wing area) (Vaughan 1959; Norberg & Rayner 1987) and wing loading (body mass multiplied by the acceleration due to gravity, all divided by wing area) (Norberg & Rayner 1987). Aspect ratio describes the shape of the wing, i.e. narrow (high aspect ratio) vs. broad (Findley, Studier & Wilson 1972; Aldridge 1986), whereas wing loading describes the general manoeuvrability of a bat by comparing the area of the wings to body weight (McManus & Nellis 1972; Norberg & Rayner 1987; Jennings *et al.* 2004).

Bats with high/above average wing loading and aspect ratios tend to be fast flying aerial hawkers (catching flying insects in open habitats) and fly high over vegetation, using narrowband calls at relatively low frequencies that do not attenuate rapidly in air (Schnitzler & Kalko 1998). Conversely, bats with low wing loading and aspect ratio tend to be slow-flying aerial hawkers or gleaners (taking non-flying insects from vegetation). They often fly in cluttered environments, using low-intensity FM calls, which can detect insects at a shorter range, or use HDC echolocation involving calls

with CF components that can detect prey in clutter (Schnitzler & Kalko 1998). The wing morphology of a bat can indicate their behaviour around artificial lighting and this will be discussed further in sections 1.10.1 and 1.10.2.

It is important to understand how ALAN affects bats as they are nocturnal organisms and in Britain are protected species under Schedule 5 of the Wildlife & Countryside Act 1981 and the Conservation (Natural Habitats, &c.) Regulations 1994, that also offers protection across European Union (EU) countries. Bats are also important bioindicators as they are easy to monitor, provide key ecosystem services and are susceptible to a range of stressors (Jones *et al.* 2009; Jones 2012). I will focus on insectivorous bats in my thesis.

Early studies investigating the effects of ALAN on bats were observational, identifying insectivorous bats feeding on the insects attracted to street lights (Griffin 1958; Shields & Bildstein 1979; Fenton, Merriam & Holroyd 1983; Belwood & Fullard 1984; Geggie & Fenton 1985; Haffner & Stutz 1985; Baagøe 1986; Schnitzler *et al.* 1987; Furlonger, Dewar & Fenton 1987; Kronwitter 1988; Barak & Yom- Tov 1989; Rydell 1991; Hickey, Acharya & Pennington 1996). In Sweden *Eptesicus nilssonii, Nyctalus noctula, Pipistrellus pipistrellus* and *Vespertilio murinus* bats were observed foraging around street lights, whereas *Myotis* spp. and *Plecotus auritus* were only observed away from street lights. The spectral output of the light influenced the densities of the bats attracted to each of the street lights, with densities of 5.52 and 0.52 bats km^{-1} for HPMV and LPS/HPS street lights respectively. Insect activity was also higher at HPMV street lights compared to either the LPS or HPS lights (Rydell 1992).

In Scotland, there was significantly more activity of *P. pipistrellus* at HPMV, compared to LPS street lights. This increase in bat activity was significantly correlated to an increase in insect activity (Blake *et al.* 1994). HPMV lights emit many short wavelengths including those in the UV part of the spectrum, which are highly attractive to insects (see section 1.9).

Following on from these observational studies, there have been several key experimental studies on the effects of ALAN on bats in which ALAN alone was manipulated and causation can hence be determined. A study in south-west England set up HPS street lights in previously unlit areas close to *Rhinolophus hipposideros*

maternity colonies: bat activity was negatively affected by the presence of HPS street lights (Stone, Jones & Harris 2009). A similar study with LED street lights found that they had a negative effect on the activity of *R. hipposideros* and *Myotis* spp. but no effect on the activity of *Nyctalus/Eptesicus* spp., *P. pipistrellus* and *Pipistrellus pygmaeus* (Stone, Jones & Harris 2012).

A study in France that investigated bat activity around HPMV and LPS street lights, compared to unlit areas, also found that the effects of street lighting varied with species. Generally street lights had a positive effect on the activity of *E. serotinus, N. noctula, P. pipistrellus, Pipistrellus kuhlii* and *P. pygmaeus,* but a negative effect on the activity of *Myotis* and *Plecotus* spp. (Lacoeuilhe *et al.* 2014).

These differences in responses to ALAN between bat species resulted in the use of two terms: “light-opportunistic” and “light-averse” bat species. These terms have succeeded earlier terms, such as, “light-tolerant” or “light-exploiting” and “light-intolerant” as they seem more appropriate at describing how bats behave around artificial lights (Voigt *et al.* 2018).

1.10.1. Light-opportunistic bat species

A large number of species are classified as “light-opportunistic” (Voigt *et al.* 2018): these bats are often attracted to street lights as they provide a reliable food resource (Rydell 1992; Blake *et al.* 1994). This is known as the attraction-by-insects hypothesis i.e. the bats are feeding on the insects that are attracted to the street lights (Voigt *et al.* 2017). In Europe, these bats typically belong to the genera *Eptesicus, Nyctalus* and *Pipistrellus* (Rydell & Racey 1995) and have high/above average wing loading and high/above average aspect ratio (Norberg & Rayner 1987; Schnitzler & Kalko 1998) and share traits including aerial hawking, feeding in open habitats and emerging relatively early after sunset, which coincides with the peak availability of insects (Jones & Rydell 1994). Although all these bat species are aerial hawkers, *Eptesicus* and *Nyctalus* species are relatively large (10-30 g) and typically fly above street lights, diving near the light cone to feed on insects (Rydell 2006; Jung & Kalko 2010). *Pipistrellus* species are relatively small (<10 g) and can manoeuvre around street lights, hunting in and outside of the light cone (Rydell 2006; Jung & Kalko 2010). Alternatively, the attraction-by-artificial-light-hypothesis

states that bats are drawn to artificial lights for other reasons than foraging on insects, such as inspecting novel items, or becoming disoriented in the presence of artificial lights (Voigt *et al.* 2017).

It is important to note that even bats such as *P. pipistrellus* and *P. pygmaeus* that are considered light-opportunistic spend the majority of their time in dim or dark areas (Hale *et al.* 2015) and the presence of artificial lights has been shown to delay roost emergence (Downs *et al.* 2003). Vegetation refuges, such as those provided by tree cover are important for habitat connectivity and could help to reduce the negative effects of artificial lighting, such as increased predation risk (Mathews et al. 2015; Straka et al. 2019). Light-opportunistic bats are therefore likely to only use lights if the benefits associated with increased foraging success outweigh the perceived risk of predation (Rydell & Racey 1995).

1.10.2. Light-averse bat species

Conversely a number of bat genera, including *Myotis, Plecotus* and *Rhinolophus* are considered “light-averse” (Voigt *et al.* 2018). Light-averse species tend to have relatively low wing loadings and aspect ratios, which means they are slow flying and manoeuvrable bats (Norberg & Rayner 1987; Jennings *et al.* 2004). These bat species produce echolocation calls suitable for short range detection of insects; *Myotis* and *Plecotus* species produce broadband calls, whereas *Rhinolophus* species emit high constant frequency calls (Rydell & Racey 1995). These species typically feed by slow aerial hawking and/or gleaning, foraging along linear features and cluttered environments, but avoiding open spaces (Norberg & Rayner 1987; Rydell & Racey 1995; Ekman & de Jong 1996; Jennings *et al.* 2004). Light-averse bats also emerge later after sunset than fast flying bats; this is thought to reduce predation risk (Jones & Rydell 1994).

A major concern is that artificial lights will have long-term effects on light-averse species: if lights delay emerging times peak food availability may be missed or foraging periods shortened, which could prevent nutritional requirements being met (Boldogh, Dobrosi & Samu 2007). Moreover, if bats avoid regular commuting routes, travelling further than usual, energy expenditure may increase, which could in turn have potential fitness costs (Tuttle 1976; Kuijper *et al.* 2008; Stone, Jones & Harris

2012). For instance, in lit areas juvenile *Myotis emarginatus* and *Myotis oxygnathus* had significantly shorter forearm lengths and lower body masses than in unlit areas. While the forearm length difference disappeared by September, the body mass differences did not (Boldogh, Dobrosi & Samu 2007). These results indicate that the females either delayed parturition or that artificial light negatively affects growth rate, perhaps by reducing maternal milk supplies, although the consequences for survival are unclear.

Although the majority of studies focus on temperate insectivorous bats, a study on *Carollia sowelli* found that artificial lighting also has detrimental effects on frugivores (Lewanzik & Voigt 2014). *C. sowelli* individuals were more likely to forage in unlit areas even in low light intensities (4.5 lux). Unlike insectivores that can directly benefit from foraging on phototactic insects attracted to street lights, frugivores cannot; in fact, there is an increased risk of predation when feeding in light, so it makes sense for them to prefer to feed in unlit areas (Lewanzik & Voigt 2014).

Furthermore, artificial lighting does not always have a binary effect on bat species, as seen in the neutral effect of LED lights on *Nyctalus* spp. and *P. pipistrellus* activity, species that are both classified as light-opportunistic (Stone, Jones & Harris 2012). It is important when making comparisons on the ecological impact of artificial lights that the lighting types investigated are of comparable intensity. Moreover, it is likely that the effect of ALAN on bats will also depend on the bat's nutritional status and reproductive state (Voigt *et al.* 2018). Bats take more risks, such as emerging earlier after sunset and therefore potentially increasing the possibility of predation, when lactating or when body reserves were low due to consistently reduced ambient temperatures (Duvergé *et al.* 2000).

1.11. Effects of spectra

As well as generally investigating the impact of street lights on bats, many studies have also explored how varying the spectral output of the street light can affect bat activity. As explained in section 1.9, the range of wavelengths that a street light emits can have profound effects on a diversity of insects, many of which are preyed on by a number of bat species. A large-scale experiment in the Netherlands found no difference between moth attraction to white, green and red LED lights, but there was an increase in the activity of *P. pipistrellus* between the green and white lights compared to unlit sites (Spoelstra *et al.* 2015). A further study investigating a broader range of bat species found less activity of light-averse *Myotis* and *Plecotus* spp. under white and green lights compared to unlit sites, but not under red light. In contrast, there was more activity of light-opportunistic *P. pipistrellus* under white and green lights, compared to unlit sites, but not under red light. The increase in *P. pipistrellus* activity under green and white lights is probably due to the increase of insect activity at these lights. It seems that red lights have fewer short wavelength emissions and so are less attractive to insects and hence the bats that prey on them. The authors recommend the installation of red LED lights to mitigate the detrimental effects of ALAN on light-averse species (Spoelstra *et al.* 2017). However, a more recent study demonstrated that even red street lights will deter the light-averse *Rhinolophus hipposideros* bat, highlighting the importance of avoiding generalising for a number of bat species and the potential of a scale of light “averseness”, i.e*. R. hipposideros* might be more light-averse than *Myotis* spp. (Zeale *et al.* 2018).

There have been two switch-over studies prior to this thesis that have compared the spectral output of street lights on bat activity. These studies have used a before-after-control-impact (BACI) approach (Green 1979; Stewart-Oaten, Murdoch & Parker 1986). This kind of experimental design works well for large-scale studies estimating the impact of natural or human-induced alterations to a system (Conner *et al.* 2016). BACI experiments enable the calculation of the differential change, i.e. the mean difference between treatment and control sites after the “alteration” (i.e. in this case a switch-over to another lighting technology) minus the mean difference between treatment and control sites before the “alteration” (Stewart-Oaten, Murdoch & Parker 1986; Bence *et al.* 1996; Conner *et al.* 2016). BACI experiments therefore

control for both spatial and temporal differences, i.e. in these studies, these include habitat, weather and seasonal changes, which can all affect bat behaviour (Conner *et al.* 2016). A switch-over from LPS to MH street lights resulted in a significant increase in the activity of *Nyctalus* spp. and *P. pipistrellus* (Stone *et al.* 2015), whereas I found no difference in the activity of light-opportunistic species when street lights were switched from LPS to LED lights (chapter two). Moreover, a switch-over from HPMV to LED lights recorded a 45% decrease in *P. pipistrellus* activity, no change in *P. nathusii*, *P. pygmaeus,* or *Nyctalus/Eptesicus/Vespertilio* spp. activity, and an increase in the activity of *Myotis* spp. (Lewanzik & Voigt 2017). All these studies demonstrate that it is not just the presence of a street light that can affect bat activity, but also its spectral output. As both MH and HPMV lights emit UV wavelengths, they are more attractive to insects than either LPS or LED lights. This explains why the switch-over from LPS to MH lights resulted in an increase in *Nyctalus* spp. and *P. pipistrellus* activity, but the switch-over from HPMV to LED lights resulted in a decrease in activity of *P. pipistrellus*. However, as neither LPS or LED lights contain UV emissions, it is possible that both lights are equally attractive to insects and so the light-opportunistic bat species that prey on them, which is why there was no change in bat activity when the street lights were switched from LPS to LED lights. Furthermore, the increase in activity of the light-averse *Myotis* spp. at LED compared to HPMV lights could be because without UV emissions, the LED lights are less visually disturbing to *Myotis* spp., which enables them to fly close to the street lights (Lewanzik & Voigt 2017). It is important that perceived light intensities over a wide range of wavelengths may also change under switch-overs and disentangling the effects of spectral changes from changes in intensity cannot always be straightforward.

The spectral output of the street light is important in reducing the effects of ALAN. Blue light causes more light pollution than longer wavelengths, such as green or red light, due to the increased effect of Rayleigh scattering. This describes the process whereby shorter wavelengths will scatter more into the atmosphere than longer wavelengths (Benenson *et al.* 2002; Falchi *et al.* 2011). Short wavelengths such as blue and UV light are also typically more attractive to insects than longer wavelengths, so they have the propensity to have a greater effect on biodiversity (van Langevelde *et al.* 2011). Blue light has also been shown to be more disruptive

to the circadian rhythm of many organisms (Falchi *et al.* 2011). Therefore, the amount of blue light emitted from a street light should be reduced as much as possible, such as by avoiding the use of cool LED street lights (CCT ≥ 5000 K) in favour of neutral (CCT ~4000 K) or warm (CCT ~ 2700 K) LED lights (Longcore *et al.* 2015).

1.12. Mitigation strategies

The most effective way to reduce ALAN is to avoid installing street lights in the first place and to conserve dark areas (Gaston *et al.* 2012). However, as street lights are often considered essential in areas occupied by humans, and with increasing urbanisation and industrialisation taking place on a global scale, it is likely that the number of street lights will continue to increase.

As street lights are important for humans' perceived security (Lyytimäki *et al.* 2008), the complete removal of street lights is unlikely in many areas, particularly those that are in densely populated areas. It is therefore more realistic to implement mitigation strategies that can help to reduce the ecological impact of ALAN. Many of the mitigation strategies adopted by local authorities are primarily implemented for their financial benefits, but many have the potential to have a positive effect on a number of nocturnal species (Gaston *et al.* 2012).

A number of mitigation strategies can easily be implemented with LED street lights as many are fitted with a central management system (CMS), which means that operators can remotely and in real-time control the street lights (Gaston *et al.* 2012). For example, street lights could be completely switched off during periods of the night when there is little human activity, a strategy known as part-night lighting (PNL) (Day *et al.* 2015). The issue for bats and many other nocturnal species is that their periods of peak activity are at dusk and dawn, times at which the street lights are still switched on, so the ecological benefits of PNL strategies seem limited (Gaston *et al.* 2012). This has been shown to be the case for light-averse *Rhinolophus ferrumequinum*, which has a bimodal activity pattern, with a first peak one hour after sunset, followed by a smaller peak at the sixth/seventh hour after sunset. After modelling a number of scenarios, PNL was only effective for *R. ferrumequinum* if street lights were switched off before midnight (Day *et al.* 2015), but in reality, most

lights are switched off between midnight and 5.30 am (Stone 2013). An experimental study in France also found that PNL schemes were not ecologically beneficial as they had no effect on the activity of five out of eight species of bats studied (Azam *et al.* 2015). However, PNL did have a positive effect on the activity of light-averse *Plecotus* spp., which is why it is important to consider the ecological impacts of ALAN at a species-specific level (Azam *et al.* 2015).

Another mitigation strategy is to reduce the intensity of the street lights using dimming. Dimming reduces the amount of light distributed from the light source, creating dark corridors that light-averse species could use for foraging and commuting (Gaston *et al.* 2012). The effectiveness of dimming on nocturnal species will also depend on the organisms' sensitivity to light. It is challenging to obtain a light level that is suitable for human vision, has economic benefits and ecological advantages (Gaston *et al.* 2012). As I show in chapter three, there was no difference in the number of bat passes under unlit lights and street lights dimmed to 25% of their original output. However, this study took place in a suburban habitat and contrasts with a study that explored the effects of dimming in rural areas that were previously unlit. Stone, Jones & Harris (2012) found that even at low lux levels (3.6 lux), the light-averse species *Myotis* spp. and *R. hipposideros* were negatively affected by street lights.

1.13. Rationale

Globally, there is a current trend to switch from narrow spectrum street lights, such as low-pressure (LPS) and high-pressure (HPS) lights, to broad-spectrum "white" lights, mainly LED lights, but also to fluorescent (FL) and metal halide (MH) lights (De Almeida *et al.* 2014; Rowse, Harris & Jones 2016; Wakefield *et al.* 2017). Although the lighting industry describes these broad-spectrum technologies as "environmentally friendly" (Stone, Jones & Harris 2012; Wakefield *et al.* 2017), this term is slightly misleading because it focuses on reduced greenhouse gas emission and increased energy efficiency but fails to consider the ecological impacts of these broad-spectrum light sources. It is these ecological impacts that I am interested in exploring further to determine how ecologically, as well as environmentally, friendly

these broad-spectrum lights are. LED lighting is predicted to continue to grow at an increasing rate and as a result will be the focus of my thesis.

1.14. Thesis aims and plan

My overall aim is to investigate the impact of modern lighting technology, namely the effect of LED street lights on bat activity. I aim to provide recommendations that will mitigate the detrimental impacts of ALAN on wildlife and ensure adequate lighting requirements for humans, whilst also being economically viable.

In chapter two I used a before-after-control-impact study to compare bat activity and feeding behaviour around LPS and LED street lights. I carried out this switch-over study at 12 sites across southern England. My three main objectives were to determine: i) if the switch-over from LPS to LED street lights caused an increase or decrease in the activity of all species; ii) if the switch-over from LPS to LED had varying effects on the activity of individual species; and iii) if the switch-over from LPS to LED caused an increase or decrease in the proportion of feeding buzzes relative to echolocation calls for bat species.

In chapter three, I examined whether changes in the intensity of LED street lights affected bat activity by considering light-opportunistic and light-averse species separately. I carried out a study at 21 sites across Hertfordshire, south-east England to test the following two hypotheses: i) bat activity of the light-opportunistic bat *P. pipistrellus* will decrease at dimmed LED lights compared to undimmed LED lights due to reduced insect abundance at dimmed street lights; and ii) bat activity of light-averse species from the genus *Myotis* will increase at dimmed LED lights compared to undimmed LED lights because the reduced light distribution will create dark refuges for light-averse bats to forage and commute.

In chapter four, I explored the UV ocular transmission in the eyes of some British bat species and inferred the implications of switching to modern street lighting technologies, including LED, MH and FL lights. I tested two hypotheses: i) there would be differences in the UV transmission between light-opportunistic and light-averse bat species. I predicted that light-opportunistic bat species would have more

UV transmissive lenses than light-averse species as they spend more time foraging in lit environments compared to light-averse species; and ii) the lenses of rhinolophid bats are less UV-transmissive than vespertilionid bats because, unlike rhinolophids, vespertilionid bats have a UV-tuned SWS visual pigments and so are more likely to benefit from lenses that transmits more UV wavelengths.

In chapter five I reflect on the results from chapter two, three and four alongside existing literature to determine recommendations for helping to mitigate the detrimental effects of ALAN as well as providing suggestions for future research.

Chapter 2: The switch-over from low-pressure sodium to light-emitting diode street lights does not affect bat activity at street lights.

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Abstract

Artificial light at night (ALAN) has increased extensively over the last century. Among the main contributors are street lights. The number of street lights across the world has increased, and the range of wavelengths that they are emitting is changing. The current trend in many countries is a shift from narrow light spectrum sources such as orange low-pressure sodium (LPS) and yellow high-pressure sodium (HPS) lights to broad spectrum “white” lighting technologies such as light emitting diodes (LED). This has the potential to affect a broad range of taxa.

To determine if this was the case, I used a before-after-control-impact paired design to examine the effects of a switch from low-pressure sodium (LPS) to light emitting diode (LED) street lights on bat activity. The experiment took place at 12 suburban sites across southern England. LED lights produce broad spectrum ‘white’ light compared to LPS street lights that emit narrow spectrum, orange light. These spectral differences could influence the abundance of insects at street lights and thereby the activity of the bats that prey on them. Most of the bats flying around the LED lights were aerial-hawking species, and the species composition of bats was similar at LPS and LED lights.

The switch-over from LPS to LED street lights did not affect the activity, or the proportion of passes containing feeding buzzes, of those bat species typically found in close proximity to street lights in suburban environments in Britain. This is encouraging from a conservation perspective as many existing street lights are being, or have been, switched to LED before the ecological consequences have

been assessed. However, lighting of all spectra studied to date generally has a negative impact on several slow-flying bat species, and LED lights are rarely frequented by these “light-averse” bat species.

2.1. Introduction

Increased use of artificial lighting over the last century has resulted in extensive changes in the nocturnal landscape (Hölker *et al.* 2010a; Kyba & Hölker 2013). Although (ALAN) has anthropogenic benefits (Gaston *et al.* 2015), light pollution is widespread (Jakle 2001; Kyba *et al.* 2015; Royal Commission on Environmental Pollution 2009) and can affect organisms across a range of spatial scales (Gaston, Visser & Hölker 2015).

Street lights are widely used around the world and have the potential for far-reaching effects on the environment, biodiversity and human health (Gaston *et al.* 2012; Navara & Nelson 2007). During the first part of the 21st century, the number of street lights in the UK continued to increase by 3% per annum (Royal Commission on Environmental Pollution 2009) and their spectral signatures, i.e. the range of wavelengths that the lights emit, have changed (Cinzano, Falchi & Elvidge 2001; Schubert & Kim 2005). There is currently a shift in street lighting from narrow light spectrum sources such as LPS and HPS lights to broad spectrum “white” lighting technologies such as LED (Rydell 2006; Gaston *et al.* 2012; De Almeida *et al.* 2014) (Figure 2.1).

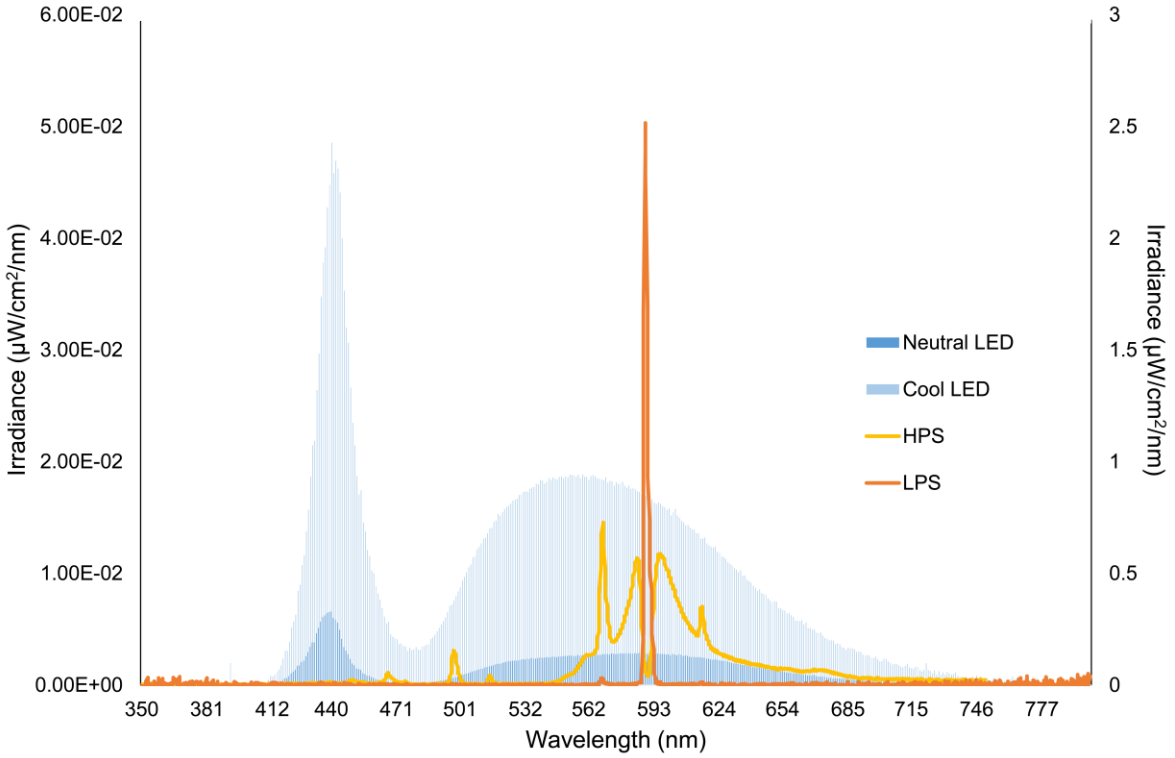

Figure 2.1. The spectral output of LPS and LED street lights, representative of the lights used in this study. LPS and neutral LED spectral outputs were taken from site J and the cool LED spectral output from site G, shown in Figure 2.2. HPS spectral output was taken from one of the sites from the HPS switch-over study.

LED lights have a number of advantages, including increased energy efficiency, directionality, controllability (ability to dim and switch-off when not in use), longevity and flexibility of colour choice (Elvidge *et al.* 2010; Gaston *et al.* 2012; De Almeida *et al.* 2014). LED lights also have a higher colour rendering index (CRI), which expresses the capacity for a light source to yield the "true" colour of an object in relation to human vision (Elvidge *et al.* 2010). Street lights exist primarily for perceived human safety benefits, and improved colour rendering for human vision enables people to see their surroundings clearly, making them feel less vulnerable at night (Lyytimäki *et al.* 2008).

While these changes in spectral output accommodate human vision, many organisms have different spectral sensitivities (Land & Nilsson 2002). Insects, for instance, are attracted to shorter wavelengths, particularly near the UV part of the spectrum, as this corresponds with the peak spectral sensitivities of their eyes (Muirhead-Thomson 1991; Eisenbeis 2006; Cowan & Gries 2009). Hence insects are

common around old technology gas discharge street lamps that contain a high proportion of short wavelengths, such as high pressure mercury vapour (HPMV) lights (Eisenbeis 2006), whereas insects are rarer around LPS lights, which are essentially a monochromatic source (Frank 2006).

Bats are a good taxon to measure the ecological impact of artificial light since they broadly exhibit species-specific responses to ALAN (Stone, Jones & Harris 2012; Pawson & Bader 2014). Street lights attract fast-flying bats such as those in the genera *Eptesicus*, *Lasiurus*, *Nyctalus* and *Pipistrellus* (Rydell 1992; Blake *et al.* 1994; Rydell & Racey 1995). These light-opportunistic bats share a number of traits including aerial hawking (Jones & Rydell 1994), foraging in open habitats (Lacoeuilhe *et al.* 2014) and emerging relatively early after sunset, which is believed to coincide with peak insect availability (Jones & Rydell 1994). *Eptesicus* and *Nyctalus* species tend to fly above street lights, diving near the light cone to feed, whereas *Pipistrellus* species hunt in and out of the light cone (Rydell 2006; Jung & Kalko 2010). *P. pipistrellus* bats spend the majority of their time in dim or dark areas (Hale *et al.* 2015; Mathews *et al.* 2015), so are only likely to use lights if the benefits associated with increased foraging success outweigh the perceived risk of predation (Rydell & Racey 1995). In contrast, ALAN is detrimental to slow-flying bats such as *Myotis*, *Plecotus* and *Rhinolophus* species (Rydell & Racey 1995; Stone, Jones & Harris 2009, 2012), which rarely feed around street lights, perhaps because the perceived risk of predation may be too high (Jones & Rydell 1994; Rydell, Entwistle & Racey 1996). A major concern is that the spread of ALAN will have long-term effects on these slow-flying, light-averse bats.

Many local authorities across Britain are in the process of switching their old LPS and HPS lights to LED lights. One of the main drivers is cost, as local authorities can save money from reduced energy use and maintenance costs. Similar changes are happening across continental Europe. However, LED lights are spectrally different from either LPS or HPS lights, the predominant street lights in the UK and around the world (Davies *et al.* 2013). Species have existed under the yellow and orange hues emitted by sodium street light for decades; how they will change following the introduction of modern broad spectrum lights is unclear (Pawson & Bader 2014). The effect of an artificial light on each organism will depend on its photoreceptors and

visual sensitivity, the spectral output of the light source, the intensity of the light and reflectance from the surrounding environment (Gaston *et al.* 2012).

My aim was to investigate how the switch-over from LPS to LED street lights affected bat activity and feeding behaviour. My main objectives were:

i) To determine if the switch-over from LPS to LED street lights caused an increase or decrease in the activity of all species.

ii) To determine if the switch-over from LPS to LED street lights had varying effects on the activity of individual species (*P. pipistrellus, P. pygmaeus* and *Nyctalus* spp.).

iii) To determine if the switch-over from LPS to LED street lights caused an increase or decrease in the proportion of feeding buzzes relative to echolocation calls for all bat species.

2.2. Methods

2.2.1. Site description and experimental set-up

A before-after-control-impact paired design (BACIP) (Stewart-Oaten, Murdoch & Parker 1986), based on a previous study (Stone *et al.* 2015), was used to examine the effects of a switch from LPS to LED street lights at 12 sites in four counties (East Sussex, Gloucestershire, Hampshire and Hertfordshire) across southern England (Figure 2.2). Originally, I contacted 39 councils to find out which counties were carrying out switch-overs in a timeframe that corresponded to the peak bat activity (i.e. May- September). In addition to the 12 sites that switched from LPS to LED street light, four sites in three counties (Berkshire, Gloucestershire and Somerset) switched from HPS to LED lights. While I collected data for these sites, my focus for this chapter is the switch-over from LPS to LED street lights because of the limited number of samples for the HPS to LED light switch-over.

A BACIP identifies if the impact being tested affects the system in question as it controls for variables such as environmental factors and seasonal changes (McDonald, Erickson & McDonald 2000), and so it was essential that the control and

experimental lighting columns were matched as closely as possible. I used existing street lights and so site choice was governed by where local authorities were switching from LPS to LED street lights. Each site consisted of a pair of lighting columns, one control (remaining LPS throughout the study) and one experimental (changing from LPS to LED). Control columns were restricted to areas where LPS lights remained the dominant street lights throughout the study, whereas experimental columns were restricted to areas where LPS lights were the dominant lighting type before switch-over and LED lighting after switch-over. Paired columns were separated by a mean distance of 1.40 km (SD ± 0.90 km) to reduce the chance of recording the same bats around the control and experimental lighting columns. Experimental columns were separated by a mean distance of 113.50 km (SD ± 60.70 km) to ensure the samples were independent and representative of a range of habitat types.

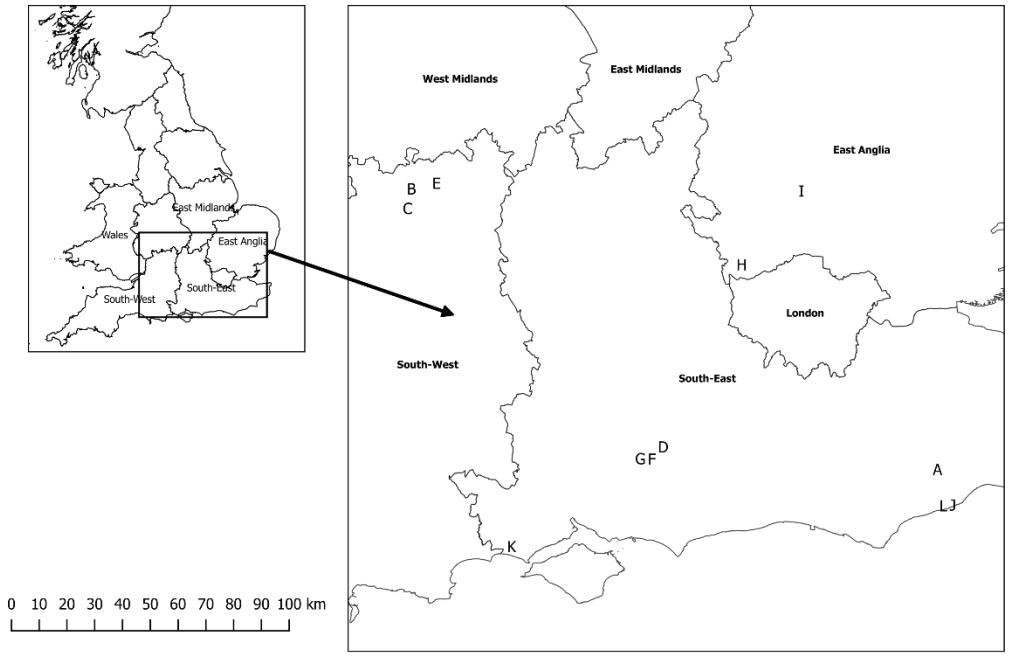

Figure 2.2. Locations of the 12 study sites in southern England. There were two lighting columns at each site, one control, the other experimental.

All sites were in suburban habitats close to bat commuting and foraging habitats (Gaisler *et al.* 1998); ten sites were in residential areas, the other two (sites H and I) were on A-class roads. Aerial imagery on Google Earth was used to match the distance to wooded areas, freshwater and grassland as closely as possible between the control and experimental columns (Table 2.1), although some variation was inevitable because this was a "real-life" experimental set-up. To ensure that the implications of imperfect pairings did not have significant consequences on my results, I carried out more complex statistical analyses (Results section 2.3.3). However, all sites were no greater than 118 m from a wooded area, defined as >10 trees (mean 52.40 m, SD ± 32.00 m), 450 m from a freshwater source (mean 220.10 m, SD ± 182.20 m) and 650 m from grassland (mean 115.30 m, SD ± 154.40 m). Within sites, there was a mean difference between the control and experimental columns of 35.40 m (SD ± 32.60 m) between distance to a wooded area, 130.40 m (SD ± 144.00 m) to a freshwater source and 107.40 m (SD ± 181.40 m) to grassland.

Table 2.1. Specifications of the LPS and LED street lights used in this study. Control and experimental lighting columns in each pair were matched in terms of height (m) and output (watts) prior to switch-over. For the experimental columns, the output and illuminance readings of the LED lights after switch-over are shown in brackets. Proximity to key habitats is shown for each column. Letters denote the 12 study sites; the location of each site is shown in Figure 2.2. Power (watts) can reduce, but illuminance (lux) can stay the same or increase after the switch-over to LED lights. This is because LED lights are more energy efficient and the lanterns are more directional than LPS lights.

Site	Column	Column height (m)	Power (watts)	Illuminance (lux)	Distance to a wooded area (m)	Distance to freshwater (m)	Distance to grassland (m)
A	Control	6	55	41	22	71	339
A	Experimental	5	35 (14)	28 (28)	56	258	161
B	Control	5	35	28	45	515	51
B	Experimental	5	35 (19)	31 (71)	91	465	28
C	Control	5	35	3*	55	55	67
C	Experimental	5	35 (27)	3* (57)	78	413	25
D	Control	5	26	8*	60	390	131
D	Experimental	5	26 (10)	3* (20)	52	333	46
E	Control	5	35	36	36	29	64
E	Experimental	5	35 (27)	31 (60)	154	161	9
F	Control	5	26	28	46	53	58
F	Experimental	5	26 (10)	41 (20)	54	90	135
G	Control	5	26	2*	81	59	30
G	Experimental	5	26 (10)	3* (19)	91	59	82
H	Control	10	91	60	87	215	17
H	Experimental	10	91 (107)	60 (109)	17	397	16
I	Control	10	91	118	7	14	55
I	Experimental	10	91 (107)	114 (178)	59	68	2
J	Control	5	35	29	31	206	127
J	Experimental	5	35 (14)	40 (29)	4	175	177
K	Control	5	26	2*	50	252	163
K	Experimental	5	26 (10)	28 (18)	33	709	156
L	Control	5	35	41	38	137	746
L	Experimental	5	35 (14)	40 (25)	50	157	81

* These are only approximate measurements of illuminance as these street lights had old-fashioned omni-directional lanterns, so it was not possible to obtain an accurate illuminance reading at these sites (Supplementary material, Figure S2.1).

Control and experimental columns in each pair were matched for height (m), output (watts) and illuminance (lux). The local authorities provided information on the light type, output and column height. Within sites, the column heights, light type and output were identical between the control and experimental columns except for site A, where the control column was 6 m in height and had an output of 55 watts, whereas the experimental column was 5 m in height and had an output of 35 watts (Table 2.1).

Light measurements from control and experimental lighting columns were taken with a lux meter (photometric system) and a spectrometer (radiometric system) to ensure that the light output and intensity of the paired street lights were comparable. Illuminance was measured with a TES 1330 lux meter (ATP Instrumentation Ltd, Leicestershire, UK) held horizontally 1.8 m from the ground directly beneath the street light. Irradiance (absolute intensity of the street light) was measured ($\mu W/cm^2/nm$) 4 m directly below the lantern with a tripod and using a calibrated Ocean Optics USB 2000 spectrometer, a P200-5-UV/VIS patch cord and a CC-3 cosine corrector. A Gershun tube was used to reduce the acceptance angle (the amount of light that falls on the sensor) to ensure that the irradiance measurement was from the street light. Ensuring all light readings were taken 4 m from the lantern enabled absolute intensities to be compared between columns of varying heights. Since environmental variables such as temperature, precipitation and cloud cover affect light readings (Institution of Lighting Engineers 2007), I took light measurements on clear dry nights when there was no full moon.

2.2.2. Measuring and identifying bat calls

Field work took place between May and October 2014. Bat activity was measured using Song Meter SM3 Bat Recorders (Wildlife Acoustics Inc., Massachusetts, USA). Prior to deployment all detectors were tested in a semi-anechoic chamber and the microphone placed 1 m and at an angle of 45° from the speaker of an ultrasound generator, which then played a series of high frequency sounds between 20 and 120 kHz. All detector systems used were comparable in sensitivity as determined by visual inspection of waveforms in BatSound (Pettersson Elektronik, Uppsala Science Park, Sweden). Four detectors were used to further minimise bias: they were

randomised between sites, but the same detector was used before and after switch-over for both the control and experimental lighting columns.

Street sign and tamtorque sign fixing clamps were used to attach the bat detectors on average 1.09 m (range 0.73 m to 2.07 m) from the lantern to ensure a standardised method across lighting columns (Figure 2.3). Recordings were made simultaneously at both the control and experimental columns for three consecutive nights before and after the switch-over. Bat detectors were set to record bat activity using triggers from 30 minutes before sunset on the first night until 30 minutes after sunrise on the fourth morning. The microphone on the detector was pointing in the same direction as the lantern. All detectors ran the same program, which was generated on SM3 Configurator 1.2.4 (Wildlife Acoustics Inc. 2015) and files were stored as waveform audio files (WAV). The settings on the detectors were: high pass filter 16 kHz; sample frequency 384 kHz; minimum frequency 16 kHz; maximum frequency 120 kHz; maximum recording time 15 seconds; and trigger level 12 dB. Detectors were removed between treatments and post switch-over recordings were made a minimum of seven days (mean 14.90 days, SD ± 5.30 days) after conversion to enable the bats to adjust to the new lights (Stone *et al.* 2015).

Figure 2.3. The typical arrangement of the SM3 bat detector and microphone on a lighting column 1m below the lantern.

It is not possible to record individual bats using acoustical methods, so bat activity was monitored as the number of passes over the three recording nights. A bat pass was defined as when the time between pulse intervals was four times the interpulse interval (Parsons & Jones 2000; Stone, Jones & Harris 2009, 2012). I also investigated bat feeding behaviour around the control and experimental columns. Before catching an insect, a bat produces a feeding buzz, which is distinguishable from other echolocation calls by its higher repetition rate (Rydell, Entwistle & Racey 1996; Britton *et al.* 1997). Relative feeding activity was measured using a "buzz ratio", which is the proportion of call sequences that included feeding buzzes over the three recording nights (Vaughan, Jones & Harris 1997). Buzz ratio acted as a proxy for insect activity, the assumption being that the higher the buzz ratio, the more attractive the light source was to insects. I used buzz ratios as a measure of feeding relative to general activity at LPS and LED street lights.

I analysed the bat calls using the automatic identification software programme Kaleidoscope Pro (v0.1.1.20, Wildlife Acoustics Inc., Massachusetts, USA) with British Bat Classifiers (v1.0.5). All bat calls were also validated manually using Kaleidoscope viewer and Bat Sound using the parameter values stipulated in Russ (2012) to ensure correct identification. Manual validation was used to record multiple

passes and/or species per file. Bats were identified to either species (*Eptesicus serotinus*, *Pipistrellus nathusii*, *P. pipistrellus* and *P. pygmaeus*) or species groups (*Myotis* spp., *Nyctalus* spp. and *Plecotus* spp.) depending on how diagnostic the calls of particular species were (Walters *et al.* 2012).

2.2.3. Measuring insect activity

At four sites, I also installed sticky traps to determine the number of insects attracted to both LPS and LED street lights. Sticky traps were made with a Fasson S692N sheet (a general purpose permanent acrylic adhesive) overlaid on corrugate plastic sheets (30 x 15cm). Sticky traps were attached simultaneously for one night at both the control and experimental light columns, both before and after the switch-over. I only included nights with temperatures at sunset above 10^{o}C and without precipitation. Insect traps were put up at sunset and removed at civil dawn (30 minutes before sunrise, when the centre of the sun is 6 degrees below the horizon) to ensure that only nocturnal insects (i.e. the insects that are likely to be eaten by bats) were collected. I only erected sticky traps on four of the lighting columns because this idea was explored mid-way through the field season after I noticed that insects were being attracted to LPS lights, contrary to the findings of Rydell (1992) and Blake *et al.* (1994). I could only attach the sticky traps at lighting columns that were <6 m, otherwise I would have required assistance from the councils to attach and remove the traps. As soon as the sticky traps were removed from the lighting columns, they were immediately frozen to preserve the specimens and subsequently identified to order level by research technician Moth Broyles. Due to the small sample size, these data will only provide additional support to the buzz ratio data when making comparisons of insect attraction between LED and LPS street lights.

2.2.4. Data analysis

The pairings were an integral part of the experimental design as they accounted for any environmental and/or seasonal changes between the two recording periods. To determine if the switch-over from LPS to LED street lights affected bat activity, I was interested in the difference in the number of bat passes before and after the switch-over between the control and experimental lighting columns (Schwarz 2014). If the LED lights did not affect bat activity, the difference between the control and

experimental column in each pair would be negligible or inconsistent between pairs (Underwood 1991).

As the bat activity data were not normally distributed, I used a series of Wilcoxon-signed rank tests to determine if there was a difference in the number of bat passes between LPS and LED street lights compared with differences in the paired control situation where no switch-over occurred. I compared bat activity of all species combined, and separately for *P. pipistrellus*, *P. pygmaeus* and *Nyctalus* spp., which contributed 90% of all recorded bat calls. Similarly, buzz ratio data were not normally distributed and so a Wilcoxon-signed rank test was used to test for differences between LPS and LED lighting columns. The buzz ratios of all species were compared, as were the data for *P. pipistrellus,* which contributed 80% of all buzz ratios recorded. Bonferroni corrections were used to adjust for multiple testing to reduce the risk of false positives; a significant difference between LPS and LED for the bat activity and buzz ratios was accepted if $p < 0.0125$ and $p < 0.025$ respectively (Altman 1991). Data collected from the HPS to LED switch-over and the insect counts were also not normally distributed and so a Wilcoxon-signed rank test was also applied. Species richness and species diversity indices (Magurran 2003) were calculated to compare relative abundances of bat species around LPS and LED street lights. All statistical and descriptive analyses were carried out in R Studio (version 0.99.451) (R Development Core Team 2013). The Wilcoxon-signed rank test was conducted using the coin package (Hothorn *et al.* 2008) and the species richness and species diversity indices were conducted using the vegan package (Oksanen *et al.* 2015).

2.3. Results

2.3.1. Bat activity

There were 30,416 files from the 12 sites (24 columns). These contained 37,124 bat passes, an average of 1.2 passes per file: 70.00% of passes were *P. pipistrellus*, 13.00% *Nyctalus* spp., 9.40% *P. pygmaeus* and 7.70% *Myotis* spp. (Supplementary material, Tables S2.1 to S2.4). However, nearly all the *Myotis* spp. calls were recorded from site E after the experimental column had been switched to an LED

light. *P. pipistrellus* were found at both control and experimental lighting columns across all sites, *P. pygmaeus* were found across all sites but only at 10 of the 12 control columns, and *Nyctalus* spp. were recorded at all control lighting columns but only nine of the experimental columns.

There was no significant difference in the number of passes from all species before and after the switch-over to LED between the control and experimental columns ($W = 30$, $Z = -0.71$, $p = 0.48$; Figure 2.4a). Bat activity was not significantly different between LPS and LED street lights for *P. pipistrellus* ($W = 30$, $Z = -0.71$, $p = 0.48$; Figure 2.4b), *P. pygmaeus* ($W = 36.50$, $Z = -0.20$, $p = 0.84$; Figure 2.4c) or *Nyctalus* spp. ($W = 35.50$, $Z = -0.28$, $p = 0.78$; Figure 2.4d). Thus the switch-over from LPS to LED street lights did not have a significant effect on either total bat activity or individual species/groups for which I had adequate data. In many cases the responses at the control and experimental lighting columns mirrored each other, i.e. when there was an increase in the number of bat passes at the control column, there was a similar increase at the experimental column and *vice versa*. Although the direction of change was consistent across 11 of the 12 sites, at sites E and I the magnitude of change at the experimental columns was greater than that at the control columns.

The results from the switch-over from HPS to LED street lights showed a similar pattern to the results from the switch-over from LPS to LED street lights. There was no significant difference in the number of passes from all species before and after the switch-over to LED from HPS ($W= 6$, $Z= 0.37$, $p= 0.72$). Bat activity was not significantly different between HPS and LED street lights for *P. pipistrellus* ($W = 6$, $Z = 0.37$, $p = 0.72$), *P. pygmaeus* ($W = 7$, $Z = 0.73$, $p = 0.47$) or *Nyctalus* spp. ($W = 5$, $Z = 1.07$, $p = 0.29$).

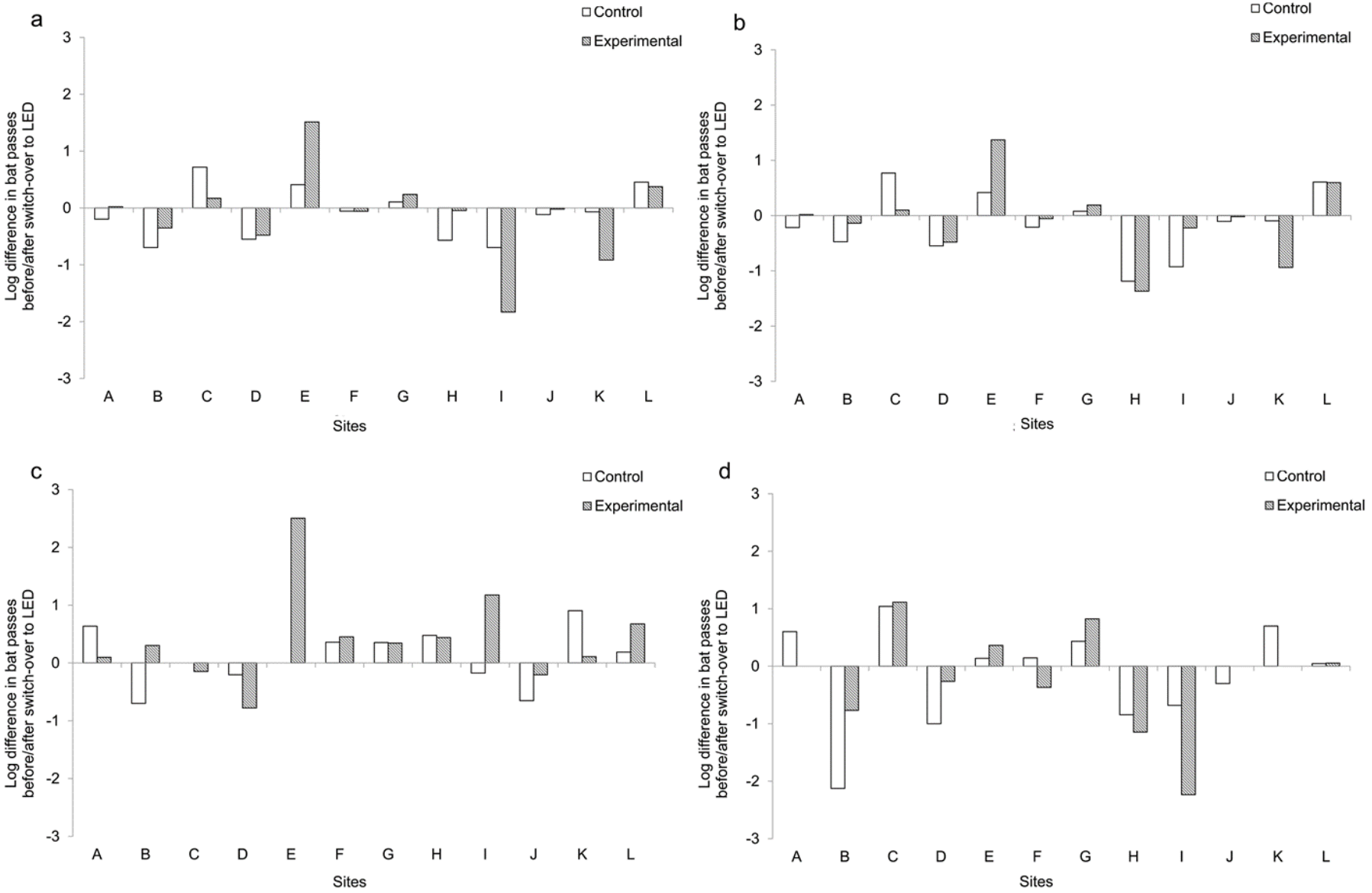

Figure 2.4. The differences in the log bat passes (number of bat passes after the switch-over minus the number of bat passes before the switch-over) for the control and experimental columns in each pair. (a) total bat activity, (b) Pipistrellus pipistrellus, (c) Pipistrellus pygmaeus and (d) Nyctalus spp. Letters denote the 12 study sites; the location of each site is shown in Figure 2.2**.**

2.3.2. Buzz ratios

There was no significant difference in buzz ratios between the LPS and LED street lights for all bat species (W = 53, Z = 1.10, p = 0.27; Figure 2.5a) or for *P. pipistrellus* (W = 46, Z = 0.55, p = 0.58; Figure 2.5b). As with the total number of bat passes, the patterns of change at each site were usually the same at both the control and experimental columns. However, there was a marked difference at site E, where there was a decrease in the buzz ratio even though the number of bat passes at the experimental site increased by more than 32 times after the switch-over to a LED light (Figure 2.5a).

2.3.3. Additional results

To ensure that I was not committing a type II statistical error and the non-parametric tests that I used had sufficient statistical power, I also carried out a Generalized Linear Mixed Models (GLMM) to enable me to include a number of factors that I consider *a priori* to be important, such as temperature (ºC), wind speed (km/hr), nightly rainfall (mm) and distance to water features (m). I used the lme4 package (Bates *et al.* 2015). Models for bat activity and insect counts followed a negative binomial distribution with a log-link function and the model for buzz ratio followed a binomial distribution with a logit-link function. Model choice was based on backward selection based on the second order information criterion (AICc) using the bbmle package (Bolker & R Development Core Team 2017). Model fit was validated using the Dharma package (Hartig 2017) to ensure that data were not overdispersed and to provide plots of residuals. Before fitting the GLMMs, I checked to see that the predictors, particularly the weather variables, were not correlated i.e. Spearman's rank correlation coefficient <0.5 (Freckleton 2002).

The fixed factors for both models included light type (LPS or LED), standardised weather variables (centred around a mean of 0 and a standard deviation of 1), mean nightly temperature (ºC), mean nightly wind speed (km/hr) and mean nightly rainfall (mm). Session (before or after) was nested within site to account for the repeated measurements within each lighting column.

The results from the GLMMs corroborated those from the Wilcoxon-signed rank test, as the number of bat passes for all species were not dependent on the switch-over from LPS to LED street lighting (χ^2= 0.03, d.f. = 1 and *p*= 0.85). Even if I exclude site E from this analysis, the number of bat passes are not dependent on the switch-over in lighting technology (χ^2= 2.11, d.f. =1 and *p*= 0.15). Buzz ratio was however dependent on the switch-over (χ^2= 256.97, d.f. =1 and *p*<0.001), so there is scope to carry out more research into this. The number of bat passes and feeding buzzes relative to echolocation calls were both dependent on proximity to water features (χ^2=4.53, d.f. = 1, *p* = 0.03 and χ^2=252.14, d.f. = 1, p <0.001, respectively).

2.3.4. Insect activity

Of the 194 insects caught on the sticky traps, the majority were from the order Diptera (67%), followed by Hemiptera (15%), Hymenoptera (6%), Psocoptera (5%), Lepidoptera (4%), Ephemeroptera (1%), Trichoptera (1%) and Coleoptera (1%). Mean insect lengths did not differ noticeably between switch-overs at control sites (3.44 mm, SD 2.73 mm (before) and 4.37 mm, SD 2.95 mm (after)), or at experimental sites (2.81 mm, SD 2.20 mm (before) and 2.80 mm, SD 1.77mm (after)). There was no significant difference in the number of insects attracted to the LPS and LED street lights (*W*= 4, *Z*= -0.37, *p*= 0.72). This probably explains why there was no difference in buzz ratios between LPS and LED lights as prey abundance appeared to be similar.

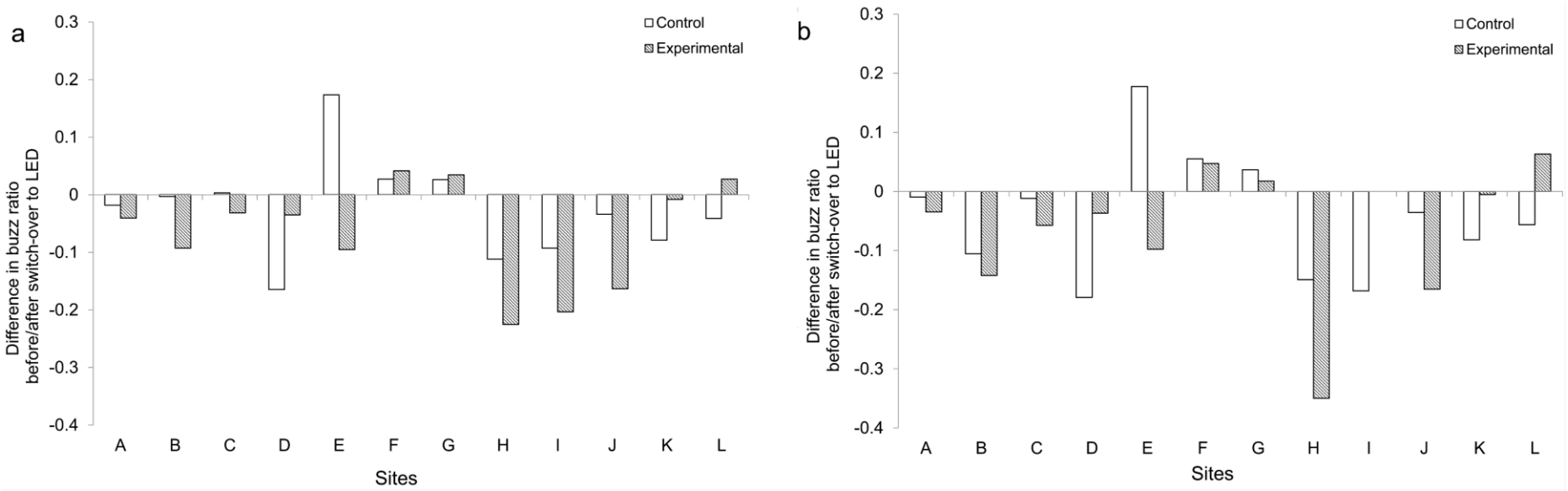

Figure 2.5. The difference in the buzz ratios (proportion of feeding buzzes after the switch-over minus the proportion of feeding buzzes before the switch-over) for both the control and experimental lighting columns. (a) all bat species and (b) *Pipistrellus pipistrellus*. Letters denote the 12 study sites; the location of each site is shown in Figure 2.2.

2.3.5. Species richness

Species richness and diversity indices showed that the same species were in the vicinity of the LPS and LED lights and diversities remained consistent across the control and experimental sites for the two time periods (Table 2.2); thus the proportion of calls per species varied little between recording periods or light type.

Table 2.2. Species richness and Shannon-Wiener, Simpson's and Fisher's alpha diversity indices before and after switch-over from LPS to LED lights.

Sites	Species richness	Shannon-Wiener index	Simpson's index	Fisher's alpha index
Control -before	8	0.93	0.51	0.89
Control - after	8	0.68	0.35	0.94
Experimental - before	8	0.81	0.45	0.88
Experimental - after	7	0.91	0.50	0.69

2.4. Discussion

The activity of all bats combined, and *Pipistrellus* and *Nyctalus* species, was not significantly different around LED and LPS street lights. This lack of difference was also apparent from the results of the HPS switch-over study, where no significant differences between total bat activity or the activity of *Pipistrellus* and *Nyctalus* species around HPS and LED street lights occurred. Moreover, I found that the buzz ratio and total number of insects did not change between the two types of street lights, again suggesting that LPS and LED lights had a similar effect on overall insect activity.

While several studies have recorded fewer bats around LPS compared to "white" street lights (Rydell 1992; Blake *et al.* 1994; Rydell & Racey 1995), the "white" lights used in those studies were HPMV street lights that, unlike LED lights, emit UV light. Compared to other spectral emissions, UV light is attractive to many insects that bats prey on. Although LED lights contain more short wavelengths than LPS lights, it is likely that both light types are equally attractive to insects since neither contains UV

light (Blake *et al.* 1994; Jones & Rydell 1994; Stone *et al.* 2015). A study in Germany that investigated the switch-over from HPMV to LED street lights demonstrated that there was a significant reduction in the activity of the light-opportunistic species *P. pipistrellus*. Although buzz ratios were not recorded in the German study, it is likely that the activity of *P. pipistrellus* decreased because fewer insects are attracted to LED lights compared to MV lights, due to the absence of UV light (Lewanzik & Voigt 2016).

In addition to LED lights, there has been interest in the ecological impacts of other new lighting technologies such as MH lights. Both MH and LED lights are broad spectrum lights and so have a high colour rendering index (Stone *et al.* 2015) but, unlike LEDs, MH lights are a gas discharge lamp and emit a high proportion of short wavelengths, including some UV emissions (Elvidge *et al.* 2010). Some local authorities are replacing LPS lights with MH rather than LED lights (Williams 2009) to save money on installation costs. Unlike my study, activity of both *Nyctalus* and *Pipistrellus* species increased around MH compared with LPS lights in a BACIP experiment with fewer study sites (Stone *et al.* 2015). However, while it was predicted that insect activity would be greater around the MH lights, the buzz ratio did not vary between the two light types, suggesting that the bats may be attracted to MH lights for some reason other than feeding. This may be related to the spectral sensitivities of bat eyes, as vesper bats can see UV light (Gorresen *et al.* 2015). Alternatively, this may be due to the limitations of the AnaBat detectors (SD1 and AnaBat II; Titley Electronics, Ballina, New South Wales, Australia) used in that study (Stone *et al.* 2015); these are less sensitive than the full spectrum Song Meter SM3 Bat Recorders I used and can fail to record the lower-amplitude parts of bat calls, such as feeding buzzes (Russ 2012). Since LED lights do not affect bat activity in any way that is different from LPS lights, replacing LPS lights with LED rather than MH lights will cause less change to bat activity around street lights.

I recorded few bats from the genera *Myotis*, *Plecotus* and *Rhinolophus*, probably because they avoid light when commuting and foraging; HPS and LED street lights showed similar effect sizes on reducing the number of passes of *Rhinolophus hipposideros* bats (Stone, Jones & Harris 2012). The low intensity echolocation calls of *Plecotus auritus* (Russ 2012), the commonest species of *Plecotus* in Britain, will

also have contributed to the paucity of data for this genus. The low numbers of *Myotis*, *Plecotus* and *Rhinolophus* bats I recorded is also likely to be attributable in part to the location of the study sites. Street lights are mostly in built-up locations, and I worked in suburban areas where there were suitable habitats for bats. However, these suburban areas are generally more open, less cluttered habitats, where slow-flying species of *Myotis*, *Plecotus* and *Rhinolophus* are less likely to occur (Norberg & Rayner 1987; Jones & Rydell 1994), although I recorded a three-fold increase in *Myotis* spp. activity at site E following switch-over. While ALAN generally has a negative effect on *Myotis* species (Stone, Jones & Harris 2012; Lacoeuilhe *et al.* 2014), this increase at the experimental site may be related to nearby swarming behaviour, which takes place in autumn (Parsons *et al.* 2003), and would explain why there was such a large increase in bat activity despite a reduction in the number of feeding buzzes. When UV lights were erected in a desert in the USA, the insects attracted to the lamps were preyed on by a number of bats, including species of *Myotis* (Fenton & Morris 1976; Bell 1980); this may be due to differences in spectral properties and intensities between the UV lamps and the LED light studied here that emitted no UV. Region is also likely to explain the low number numbers of *Rhinolophus* spp. recorded as most sites were not in south-west England or Wales, which is where *Rhinolophus* spp. are mainly found (Russ 2012).

If buzz ratio is a good proxy for insect activity, my results suggest that there is no difference in the absolute, but not necessarily relative, abundance of the groups of insects eaten by the species of bat I recorded (Vaughan *et al.* 1997) around LPS and LED street lights. Studies have shown variation across insects in the same order, such as Noctuidae and Geometridae moths. Whereby Noctuidae moths are attracted to shorter, rather than longer wavelengths, compared to Geometridae moths that are equally attracted to short and long wavelength light sources (Somers-Yeates *et al.* 2013). This lack of difference is supported by the insect data, which showed there was no significant difference between the total number of insects at LPS and LED street lights. It is important to note that these results are only based on four sites, but it is encouraging that they agree with the buzz ratio data. While there have been no direct comparisons of insect activity around LPS and LED lights, there have between HPS and LED lights, although HPS lights have broader spectral emissions than LPS lights. However, the findings are conflicting. A study in New Zealand found that

neutral 4000 K LED lights attracted 48% more insects than HPS lights (Pawson & Bader 2014), whereas a study in Germany with a mixture of cool (6500 K) and warm/neutral LEDs (3000/4100 K) found that more insects were attracted to HPS lights (Eisenbeis & Eick 2011). Moreover, a study in England found that there was no significant difference in the total number of insects attracted to HPS and LED street lights (Wakefield *et al.* 2017). These differences may reflect differences in local insect communities, the habitats in which the studies were carried out and/or because none of the studies were broad-scale. The ecological impacts of ALAN are complex. More work is needed on how both bats and their insect prey, and other taxa, respond to different street lights before we can properly assess the ecological impacts of new lighting technologies, particularly LEDs, as these will soon be used worldwide and so have the potential for far-reaching ecological effects (Wakefield *et al.* 2015).

Due to my experimental design, there was some variation between sites in illuminance (2-178 lux) and power of the different light sources (10–107 watts), as well as the correlated colour temperature (4000–5700 K) of the LED street lights. It is possible that power and illuminance, in addition to spectral outputs, are important in determining bat activity around different street lights. However, I was unable to control for these factors because the study was carried out in a “real-life” setting, and I had to use the lighting being installed by the local authority, who were replacing the LPS lighting technologies with LED lights that were considered equivalent according to human requirements. It is difficult to measure how bats perceive differences in power and illuminance, given that these measures are based on human vision (Longcore & Rich 2004). It is also likely that as the vision of insects and bats varies, how these taxa perceive illuminance will also differ. As mentioned previously, it was not possible to take accurate illuminance measurements at every site as some LPS street lights had old fashioned omni-directional lanterns (Supplementary material, Figure S2.1), and so the illuminance values are given as a guideline to the light intensities used rather than precise measurements. A study in Germany showed that illuminance did not have a significant effect on bat activity when the street lights were switched from MV to LED lights (Lewanzik & Voigt 2017). The effect of different light intensities on bat activity will be explored in further detail in chapter three. Moreover, I do not believe that colour temperature was a confounding variable because there is

little difference in insect attraction between off-the-shelf LEDs with different colour temperatures (2700 K, 5000 K and 6000 K) (Pawson & Bader 2014; Wakefield *et al.* 2016).

To understand the effects of LED lighting on bats, and enable the results to be incorporated into lighting polices, it is important that future studies include all relevant information such as light source, output, spectral distribution, luminous flux and flicker rate (Jagerbrand 2015), as well as data on habitat quality and environmental variables. It is also important that studies should involve multiple sites in different areas to avoid drawing conclusions based on local effects.

Street lights produce light via a series of pulses and although a light source might appear constant to humans, this is likely to be different for other taxa. The critical fusion frequency (CFF) measures the threshold at which a light source is perceived as a constant stream of light, rather than a series of flashes. Broad-spectrum light sources, such as LED lights have a high flicker index compared to older lighting technologies and this might have an ecological impact (Inger *et al.* 2014). The flickering of a light can be achieved by modifying the duty cycle (DC) and frequency of a light. A recent study found that fewer nocturnal insects from a range of orders were attracted to flickering LED lights (four flickering patterns; 120 Hz/ 10% DC, 240 Hz /10% DC, 240 Hz/ 10% DC and 240 Hz/ 90% DC) compared to non-flickering LED lights (Barroso *et al.* 2017). This may have important implications for bats, particularly light-opportunistic bats that prey on many of these insects.

2.5. Conservation perspective

From a conservation viewpoint, my results are encouraging because they suggest that the large-scale replacements of LPS by LED lights currently taking place in many parts of the UK, as well as in other countries (Gaston *et al.* 2012), will not affect bat activity significantly differently from what currently occurs at LPS street lights. While there may be different impacts on other taxa, my data suggest that broad spectrum light sources such as LEDs will not necessarily have a greater ecological effect on bats than narrow spectrum lights (Gaston *et al.* 2012). However, it is important that these results are viewed alongside the wider impact of ALAN on bats. The majority of echolocation calls I recorded were from three species/groups of

bats, which are typically considered to be light-opportunistic. There have been a number of studies showing the detrimental effects of lighting on roost emergence (Downs *et al.* 2003), commuting (Stone, Jones & Harris 2009, 2012) and fitness (Boldogh, Dobrosi & Samu 2007) of a number of slow-flying bat species. Many of these are already vulnerable to habitat loss and urbanisation (Stebbings 1995), and are further disadvantaged by the spread of ALAN.

2.6. Conclusions

LED lights are widely perceived as being environmentally friendly because of their lower CO_2 emissions. The results from this paired study also indicate that the switch-over from LPS to LED street lights did not affect the activity of bat species typically found in close proximity to street lights in suburban environments in the UK. The direction of change within a pair was consistent for 11 of the 12 sites and, as this experiment was carried out at a broad geographical scale, the switch-over from LPS to LED street lights is unlikely to have an effect on bat activity. From a conservation perspective this is a positive outcome as many existing street lights are being, or have already been, switched to LED in the UK and elsewhere in the world. The lack of change in the number of feeding buzzes suggests that there was no significant change in the overall abundance around street lights of those insect groups eaten by bats, although more data are needed on individual insect groups, and how LEDs affect species interactions.

2.7. Link to the next chapter

In this chapter I have explored how the switch-over from LPS to LED street lights across suburban areas affects bat activity. In chapter three, I will determine if changes in light intensity of LED street lights affects bat activity by considering light-opportunistic and light-averse species separately.

2.8. Supplementary material

Figure S2.1. An example of an old-fashioned, omni-directional street light used in this study.

Table S2.1. The number of passes and buzz ratios for total bat activity at the control and experimental lighting columns before and after the switch-over to LED lights

Table S2.2. The number of bat passes and buzz ratios for *Pipistrellus pipistrellus* at the control and experimental lighting columns before and after the switch-over to LED lights.

Table S2.3. The number of bat passes for *Pipistrellus pygmaeus* at the control and experimental lighting columns before and after the switch-over to LED lights.

Table S2.4. The number of bat passes for *Nyctalus* spp. at the control and experimental lighting columns before and after the switch-over to LED lights.

Figure S2.1. An example of an old-fashioned, omni-directional street light used in this study.

Table S2.1. The number of passes and buzz ratios for total bat activity at the control and experimental lighting columns before (two nights) and after (two nights) the switch-over to LED lights. The buzz ratios are shown in brackets.

Site	Control				Experimental			
	Before		**After**		**Before**		**After**	
A	551	(0.17)	350	(0.15)	333	(0.07)	351	(0.03)
B	890	(0.16)	179	(0.22)	81	(0.15)	36	(0.06)
C	32	(0.06)	167	(0.07)	42	(0.05)	62	(0.02)
D	85	(0.14)	24	(0.00)	542	(0.07)	180	(0.04)
E	578	(0.10)	1485	(0.28)	421	(0.14)	13,716	(0.05)
F	578	(0.04)	508	(0.07)	599	(0.09)	525	(0.14)
G	341	(0.08)	436	(0.11)	172	(0.03)	298	(0.06)
H	473	(0.14)	128	(0.02)	656	(0.26)	589	(0.03)
I	2593	(0.15)	522	(0.05)	1963	(0.20)	29	(0.00)
J	485	(0.05)	371	(0.01)	1189	(0.29)	1137	(0.13)
K	273	(0.19)	233	(0.11)	1950	(0.16)	236	(0.15)
L	106	(0.10)	302	(0.06)	97	(0.02)	230	(0.05)
Total	6985		4705		8045		17,389	
Mean	582.1	(0.12)	392.1	(0.10)	670.4	(0.13)	1449.1	(0.06)
SD	680.3	(0.05)	377.1	(0.08)	680.5	(0.09)	3875.4	(0.05)

Excluding site E, the total, mean and SD bat passes were:-

	Control		Experimental	
	Before	**After**	**Before**	**After**
Total	6407	3220	7624	3673
Mean	582.5 (0.12)	292.7 (0.08)	693.1 (0.13)	333.9 (0.06)
SD	713.5 (0.05)	161.4 (0.06)	709.0 (0.09)	323.7 (0.05)

Table S2.2. The number of bat passes and buzz ratios for *Pipistrellus pipistrellus* at the control and experimental lighting columns before (two nights) and after (two nights) the switch-over to LED lights. The buzz ratios are shown in brackets.

Site	Control				Experimental			
	Before		**After**		**Before**		**After**	
A	546	(0.17)	332	(0.15)	329	(0.06)	343	(0.03)
B	531	(0.16)	179	(0.22)	37	(0.10)	27	(0.06)
C	26	(0.06)	153	(0.06)	35	(0.05)	44	(0.00)
D	67	(0.14)	19	(0.00)	518	(0.07)	172	(0.04)
E	555	(0.10)	1456	(0.28)	378	(0.14)	8867	(0.04)
F	435	(0.03)	269	(0.05)	563	(0.09)	495	(0.13)
G	318	(0.08)	380	(0.10)	157	(0.03)	243	(0.04)
H	416	(0.13)	27	(0.00)	420	(0.22)	18	(0.00)
I	726	(0.05)	86	(0.00)	5	(0.00)	3	(0.00)
J	470	(0.05)	369	(0.01)	1171	(0.29)	1123	(0.13)
K	271	(0.19)	218	(0.10)	1941	(0.16)	224	(0.15)
L	59	(0.08)	239	(0.06)	40	(0.00)	158	(0.04)
Total	4420		3727		5594		11,717	
Mean	368.3	(0.10)	310.6	(0.09)	466.2	(0.10)	976.4	(0.06)
SD	224.3	(0.05)	380.7	(0.09)	569.9	(0.09)	2504.1	(0.05)

Excluding site E, the total, mean and SD bat passes were:-

	Control				Experimental			
	Before		**After**		**Before**		**After**	
Total	3865		2271		5216		2850	
Mean	351.4	(0.10)	206.5	(0.07)	474.2	(0.10)	259.1	(0.06)
SD	227.1	(0.06)	127.6	(0.07)	597.0	(0.09)	324.4	(0.06)

Table S2.3. The number of bat passes for *Pipistrellus pygmaeus* at the control and experimental lighting columns before (two nights) and after (two nights) the switch-over to LED lights.

Site	Control		Experimental	
	Before	**After**	**Before**	**After**
A	3	13	4	5
B	5	0	1	2
C	0	1	7	5
D	8	5	6	1
E	1	1	6	1914
F	66	151	6	17
G	8	18	5	11
H	33	99	206	566
I	97	65	1	15
J	9	2	16	10
K	0	8	7	9
L	26	40	4	19
Total	256	403	269	2574
Mean	21.3	33.6	22.4	214.5
SD	30.6	48.1	57.9	558.6

Excluding site E, the total, mean and SD bat passes were:-

	Control		Experimental	
	Before	**After**	**Before**	**After**
Total	255	402	263	660
Mean	23.2	36.5	23.9	60.0
SD	31.4	49.3	60.5	167.9

Table S2.4. The number of bat passes for *Nyctalus* spp. at the control and experimental lighting columns before (two nights) and after (two nights) the switch-over to LED lights.

Site	Control		Experimental	
	Before	**After**	**Before**	**After**
A	1	4	0	1
B	134	0	41	7
C	0	11	0	13
D	10	0	11	6
E	19	26	26	60
F	61	85	28	12
G	14	38	6	40
H	7	0	14	0
I	1746	365	1888	11
J	2	0	0	0
K	1	5	1	1
L	18	20	45	51
Total	2013	554	2060	202
Mean	167.8	46.2	171.7	16.8
SD	498.5	103.4	540.7	21.2

Chapter 3: Effects of dimming LED street lights on light-opportunistic and light-averse bats in suburban habitats

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Abstract

Emerging lighting technologies provide opportunities for reducing carbon footprints, and for biodiversity conservation. In addition to installing light-emitting diode (LED) street lights, many local authorities are also dimming street lights. This might benefit light-averse bat species by creating dark refuges for these bats to forage and commute in urban habitats. I conducted a field experiment to determine how light intensity affects the activity of the light-opportunistic *Pipistrellus pipistrellus* and light-averse bats in the genus *Myotis*.

Higher light intensities (50% and 100% of original output) increased the activity of light-opportunistic species but reduced the activity of light-averse taxa. Compared to the unlit treatment, the 25% lighting level did not significantly affect either *P. pipistrellus* or *Myotis* spp. Light-averse bat species are often threatened, and my results suggest that it is possible to achieve a light intensity that has both economic and ecological benefits, as well as providing sufficient light for human requirements.

3.1. Introduction

Over the last 60 years, global light pollution has increased on average by 6% per annum (Hölker *et al.* 2010b). Although more prevalent in developed countries, light pollution is now considered a global threat because of increasing urbanisation and industrialisation in many developing countries (Cinzano Falchi & Elvidge 2001;

Gaston *et al.* 2012). Light pollution is the result of a number of artificially lit sources, but street lights are one of the main contributors as they are installed in most towns and cities across the world (Navara & Nelson 2007; Gaston *et al.* 2012; Kyba *et al.* 2017).

Many local authorities across Britain are replacing LPS and HPS, with LED street lights (Jagerbrand 2016). LED street lights offer a number of advantages over older lighting technologies, including increased energy efficiency, flexibility and longevity (De Almeida *et al.* 2014). In Britain, LED lights are predicted to contribute up to 70% of the outdoor and residential lighting by 2020 (Baumgartner *et al.* 2012). As well as installing LED lights, many local authorities are implementing strategies to save money and reduce carbon footprints, such as part-night lighting and dimming. In England 23% of local authorities have employed PNL schemes and 39% of them have implemented dimming regimes on a permanent basis (Campaign to Protect Rural England 2014). It is relatively easy to employ dimming regimes with LED lights because they have a rapid on/off time (De Almeida *et al.* 2014; Beccali *et al.* 2017). Dimming levels can be remotely implemented and adjusted using a central management system (CMS) (Gaston *et al.* 2012; Stone, Harris & Jones 2015). Dimming LED street lights is typically carried out by a procedure called pulse-width modulation, which manipulates the duty cycle of a signal, so that the amount of “on” time is reduced but the spectral output of the light is unchanged (Wakefield 2016; Barroso *et al.* 2017).

Bats are a useful taxon to study the ecological impacts of light because they are nocturnal and their response to ALAN varies across species. A number of species are considered “light-opportunistic” as they feed on the large numbers of insects attracted to lights (Rydell 1992; Blake *et al.* 1994). Conversely, light-averse bats, such as those species from the genera *Myotis*, *Plecotus* and *Rhinolophus*, seem to be negatively affected by all types of street lighting. Because light-averse bats are often slower flying, more manoeuvrable species (Norberg & Rayner 1987; Jennings *et al.* 2004), they may avoid light to reduce the perceived risk of predation (Jones & Rydell 1994; Rydell Entwistle & Racey 1996). Many are also of conservation concern because their wing shape limits their dispersal (Jones, Purvis & Gittleman 2003), and so they are particularly vulnerable to anthropogenic pressures such as urbanisation

and the associated ALAN. Since dimming reduces both the light intensity of the street light and the amount of light distributed from the light source (Gaston *et al.* 2012), it might create dark refuges that light-averse bats could use for commuting and foraging in urban areas (Gaston *et al.* 2012; Azam *et al.* 2018).

There are many examples of artificial lighting affecting orientation, reproduction, communication and foraging in nocturnal taxa (Lloyd 1994; Salmon *et al.* 1995; Rand *et al.* 1997; Stone, Jones & Harris 2009, 2012). However, few studies have explored the biological impacts of varying light intensities; for example, the reproduction and survival of fruit flies *Drosophila melanogaster* are negatively affected by increased light intensity (McLay, Green & Jones 2017). Increased light intensity also has a detrimental effect on the activity and melatonin level of great tits *Parus major* (de Jong *et al.* 2016) and activity patterns of blue tits *Cyanistes caeruleus* (de Jong *et al.* 2017). Increased light intensity also interrupts immune responses of Siberian hamsters *Phodopus sungorus* (Aubrecht, Weil & Nelson 2014) and Swiss Webster mice *Mus musculus* (Fonken, Weil & Nelson 2013) but does not affect sleep in *Parus major* (Raap *et al.* 2017).

Studies focussing on the effects of light intensity on bat activity have highlighted that even low light levels have a detrimental effect on the activity of light-averse bats (Stone, Jones & Harris 2012; Lacoeuilhe *et al.* 2014; Azam *et al.* 2018). Even when LED street lights were dimmed to a low level (mean 3.6 lux, range 2.90 - 4.86 lux), there were significantly fewer bat passes from the light-averse species, *Myotis* spp. and *Rhinolophus hipposideros*, than on unlit nights (Stone, Jones & Harris 2012). In France, light-averse *Myotis* spp. avoided street lights as much as 25m away, when intensity levels were below 1 lux (Azam *et al.* 2018). However, dimming street lights to an intensity below 1 lux or even 3.6 lux may not be feasible in terms of human vision and safety. Street lights exist for human safety and, if humans cannot see their surroundings clearly because the light intensity is too low, this nullifies the benefits of having street lights (Stone, Jones & Harris 2012; Lyytimäki & Rinne 2013).

My aim was to determine whether street light dimming regimes currently used by local authorities have ecological benefits for bats, as well as providing economic benefits. I tested the following two hypotheses:

1. Bat activity of the light-opportunistic bat *P. pipistrellus* will decrease at dimmed LED lights compared to undimmed LED lights due to reduced insect abundance at dimmed street lights.

2. Bat activity of light-averse species from the genus *Myotis* will increase at dimmed LED lights compared to undimmed LED lights because the reduced light distribution will create dark refuges for light-averse bats to forage and commute.

3.2. Methods

3.2.1. Experimental design

Fieldwork took place between May and August 2015 at 21 sites in Hertfordshire, in south-east England. I decided to focus my fieldwork in one county to ensure that all LED street lights were matched for model, manufacturer, illuminance (lux), power (watts) and column height (m). Hertfordshire County Council provided details of the location of all LED lights across the county. I then used aerial imagery from Google Earth and a number of site visits to select 21 sites in suburban areas that were in close proximity to bat foraging and commuting habitats (Gaisler *et al.* 1998).

All street lights used in this study were neutral LED lights (MIDI, 97 W, 4250 K, Urbis Schreder, Basingstoke, RG24 8GG, UK) that were 10 m in height. I selected street lights along tree lines that contained trees >4 m in height, and each site was at least 20 m from the beginning of the tree line (Verboom & Spoelstra 1999; Hale *et al.* 2015). All sites were also closely situated to other linear features such as hedgerows and typical bat foraging habitats including woodland areas and grassland. They were at least 35 m from a building and were located on A (major) roads in suburban areas that experienced similar traffic intensity. To ensure that dimming regimes were comparable across sites, both illuminance (lux) and irradiance (μW/cm^2/nm) readings were measured. Illuminance readings were taken using a TES 1330 lux meter (ATP Instrumentation Ltd, Ashby-de-la-Zouch, LE65 2UU, UK) at 1.8 m from the ground, directly underneath the lantern of the street light and a calibrated Ocean Optics USB 2000 spectrometer (Largo, FL 33777, USA), a 7 m P400-5-UV/VIS patch cord and a CC-3 cosine corrector, all positioned 5 m directly underneath the lantern.

Irradiance readings also allowed me to ensure that the spectral output of the street light remain unchanged and that only intensity varied with each light level (Figure 3.1).

Each site consisted of 3 lighting columns, each of which ran a series of lighting levels: 0%, 25%, 50% and 100% of the original output. Since my aim was to assess the impacts of different street lighting levels, I used three adjacent lighting columns per site to ensure that a stretch of road (at least a 60m) was subjected to the same lighting level. The street lights were dimmed using this approach, rather than modifying the intensity of the street light by a fixed proportion as it was the easiest way for the subcontractor to reduce the intensity of the street lights. The experiment ran for eight nights at each site, with the lighting level switching every two nights, i.e. each lighting level ran for two consecutive nights. The lighting schedules were randomised across sites to prevent any order effects and sites were separated by at least 1 km to ensure the collection of independent samples. The lighting levels I used were representative of differing light intensities being employed by local authorities. Light levels were controlled using pulse width-modulation by Telensa, a sub-contractor of Hertfordshire County Council using a CMS.

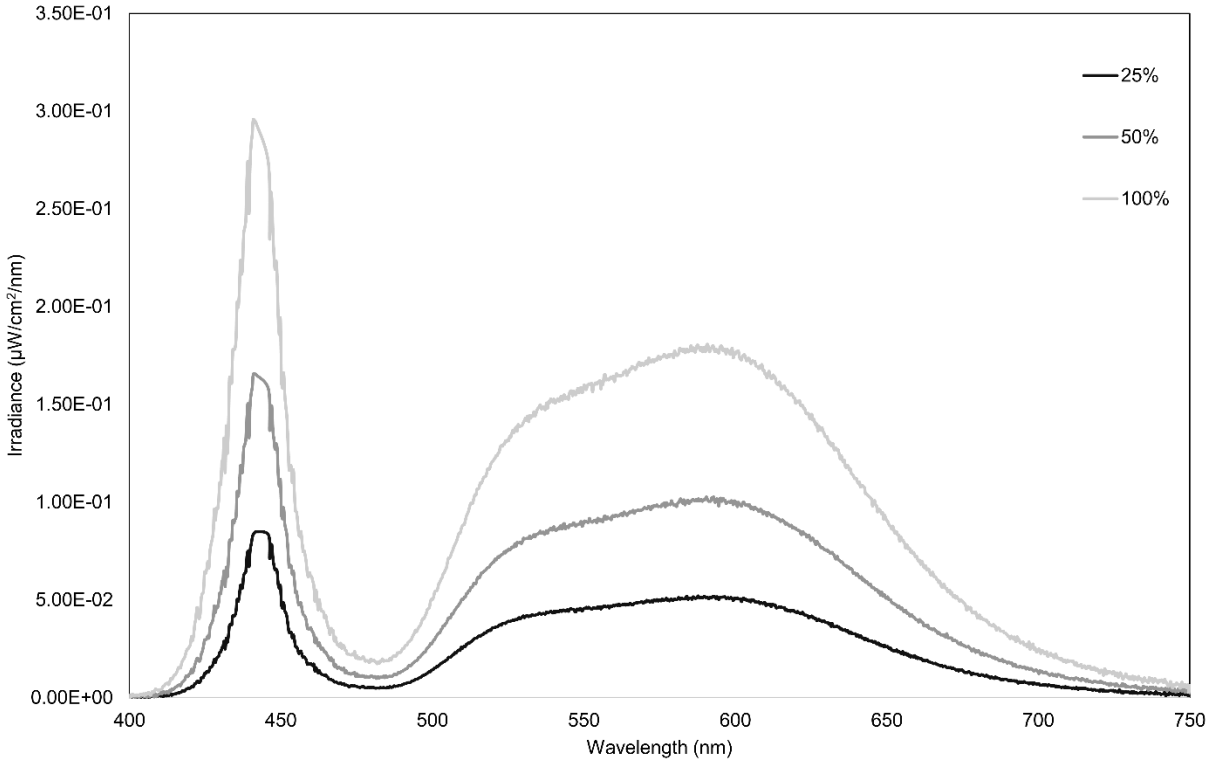

Figure 3.1. The spectral output of LED street lights at the three lighting treatments (25%, 50% and 100%) from one of the 21 sites chosen at random.

3.2.2. Detecting bat calls

I measured bat activity by monitoring echolocation calls using SM3 bat detectors (Wildlife Acoustics, Inc., Massachusetts, USA). Three sites were monitored concurrently. Bat detectors were set to record activity using triggers from 30 minutes before sunset on the first night until 30 minutes after sunrise on the ninth morning. Bat detectors were attached to the middle of the three lighting columns 1 m below the lantern, using street sign and tamtorque sign fixing clamps, with the microphone on the detector pointing slightly downwards and positioned on the same side of the column as the lantern. Bat detectors were randomised across sites. Files were stored as wavefile audio (WAV) files. The settings on the detectors were the same as those in chapter two.

Bat activity for each lighting level was measured as the number of passes over each two-night period. As there were too many sound files to go through individually (135,228 files), it was not possible to identify multiple passes per file. So, in this chapter each 15-second file was quantified as a bat pass (Mathews *et al.* 2015). At sites 19, 20 and 21 the sub-contractor failed to change the lighting level according to the agreed schedule and left the same lighting level on for three rather than two consecutive nights. In order to use the data from these sites, I only included bat passes for one recording night per treatment, rather than the usual two nights; this night was selected at random. To determine bat feeding behaviour at different light levels, I calculated the buzz ratio i.e. the proportion of passes that contained a feeding buzz using the same approach as in chapter two (Vaughan, Jones & Harris 1997) at each lighting level.

At seven sites (one from each of the three recording periods), a 12-megapixel 1080 HD Hunting Trail Infra-Red Camera (SpyCameraCCTV, Bristol, BS5 9PQ, UK) was attached to the lighting column to estimate the number of insects attracted to each lighting level. Insect activity data was collected to record the attractiveness of different LED light intensities to aerial insects, as this might provide further insight into how bat activity is affected by different light levels. Infrared cameras were used so that the number of insects could be estimated when the street lights were dimmed to low light levels (25%) or switched off (0%). The camera takes high resolution still images (12 megapixels) meaning that even small flies appeared on the images. The

camera was attached to the lighting column immediately below the lantern, so its focus was within the light cone. A burst of three still images was taken once an hour throughout the night (sunset until sunrise). These data were used to compare the attractiveness of the LED lights at different lighting levels to aerial insects.

Nightly temperature and humidity were recorded at each site with a Tinytag TGP-4017 Plus 2 Internal Temperature data logger (Gemini Data Loggers UK Ltd, Chichester, England). Mean nightly rainfall (mm) and wind speed (km/hr) were obtained from Met Office weather stations within 35 km of each site (www.metoffice.gov.uk/). The weather was broadly consistent across the eight recording nights.

3.2.3. Data processing

Due to the large number of sound files it was not possible to identify every file manually, as I did in chapter two, and so all bat calls were analysed using Kaleidoscope Pro (version 3.1.1, Wildlife Acoustics Inc., Massachusetts, USA) with British Bat Classifiers (v3.0.0). The auto-identification of *P. pipistrellus* and *P. pygmaeus* was accepted (Mathews *et al.* 2015). However, all other calls were manually identified to either species (*Eptesicus serotinus*, *Nyctalus noctula*, *Pipistrellus nathusii* and *Plecotus auritus*) or group (*Myotis* spp.); *Myotis* spp. are usually grouped because of the difficulty of separating the echolocation calls of the different species (Russ 2012; Walters *et al.* 2012; Rydell *et al.* 2017). I also manually identified files that had a margin factor of zero (either Kaleidoscope Pro was unable to identify the call or classified the call as a noise file). Margin scores in Kaleidoscope Pro are uncalibrated confidence scores, whereby higher values are more likely to be correctly identified than lower values. Species identification was verified for 676 (0.5%) of the bat echolocation call files to ensure that the auto-identification software was working effectively. These files were randomly selected across all sites to account for any differences between sites and included noise files to ensure that all files that contained a bat pass were being included in the analysis.

As I did not verify species manually from every file, I calculated the feeding buzz from a representative sample of files. For each site, I separated calls for each lighting level, then randomly selected 5% of files to check if a feeding buzz was

present (mean number of files per lighting level were 35, 44, 51 and 48 for 0%, 25%, 50% and 100% lighting levels, respectively). I identified all feeding buzzes from all species, but they were mostly from *P. pipistrellus.* All noise files were excluded as a bat pass had to occur for a feeding buzz to be present. I calculated the buzz ratio to determine how the proportion of feeding buzzes compared with the number of echolocation calls changed with light intensity.

Insect activity was determined for one night of each dimming level, when there was no rain; this was due to the difficulty in identifying the presence of insects on images when raining. Each visible white dot on the image was counted as an insect (Rydell 1992). Only insects that were within the light cone i.e. directly underneath the light were counted, and I excluded non-volant invertebrates, i.e. I did not include spiders, many of which make their webs on street lights to prey on insects attracted to the artificial light (Heiling 1999). It was only possible to estimate total insect abundance and not to identify species. The number of insects counted in each image was carried out blind i.e. I was unaware of the lighting level when counting the number of insects. The number of insects from the three images for each hour was averaged and the hourly totals then averaged over the night for each lighting level. This reduced 'noise' that might be introduced if any of the three images were unclear.

3.2.4. Statistical analyses

Data were analysed using in R Studio using R version 3.3.3 (R Development Core Team 2017). I used generalised linear mixed models (GLMMs) to determine potential drivers of bat activity, insect counts and buzz ratios using the lme4 package (Bates *et al.* 2015). Models for bat activity and insect counts followed a negative binomial distribution with a log-link function and the model for buzz ratio followed a binomial distribution with a logit-link function. Model choice was based on backward selection based on the second order information criterion (AICc) using the bbmle package (Bolker & R Development Core Team 2017). Model fit was validated using the Dharma package (Hartig 2017) to ensure that data were not overdispersed and to provide plots of residuals. Before fitting the GLMMs, I checked to see that the predictors, particularly the weather variables, were not correlated i.e. Spearman's rank correlation coefficient <0.5 (Freckleton 2002).

I used three models to analyse bat activity (bat passes); all species, *P. pipistrellus* and *Myotis* spp. For all three models the fixed factors included lighting level (0%, 25%, 50% and 100%) as well as standardized weather variables (centred around a mean of 0 and a standard deviation of 1), mean nightly temperature (°C), mean nightly wind speed (km/hr) and mean nightly rainfall (mm). Site was included as a random effect to account for repeated measurements within each lighting column. Date was also included as a random effect to account for recording at multiple sites (three sites concurrently). *Post hoc* comparisons between intermediate lighting levels (i.e. 25% vs. 50%, 25% vs. 100% and 50% vs. 100%) were carried out using multcomp package (Hothorn, Bretz & Westfall 2008) with single-step corrected probabilities.

The coefficient of determination (R^2) was calculated to compare the goodness-of-fit across the models for different bat species (Johnson 2014). In mixed-effect models, R^2 has two classifications: marginal, which is the proportion of variance in the response variable explained by the fixed effects, and conditional, which is the proportion of variance in the response variable explained by both the fixed and random effects (Nakagawa & Schielzeth 2013). R^2 values for the buzz ratio model were calculated using the MuMIn package (Bartón 2018) and the R^2 values for the bat activity and insect count models were calculated as proposed by Nakagawa, Johnson & Schielzeth (2017).

3.3. Results

Most of these passes (76.70%) were from *P. pipistrellus*, followed by *P. pygmaeus* (20.90%), *N. noctula* (1.90%) and *Myotis* spp. (0.20%), with the remaining bat passes coming from a combination of *Eptesicus serotinus* (0.08%), *Plecotus auritus* (0.08%) and *P. nathusii* (0.08%) (Supplementary material, Tables S3.1 to S3.4, Figure S3.1). No other species were recorded. From the 676 files that were manually verified, there was 87% agreement between the manual and automatic classifications, with 100% agreement with the automatic classifications of *P. pipistrellus* and *P. pygmaeus*. Kaleidoscope occasionally classified a file as a noise file or was unable to determine a classification, even when a call was present. Since

all files not classified as *P. pipistrellus* or *P. pygmaeus* were manually identified, I feel that my method was appropriate given the large amount of data collected and the time needed to analyse all the data manually.

Across the 21 sites, mean light intensities for each lighting level were 11.35 lux (SD 3.23, range 8.68 - 14.90 lux) for 25%, 20.23 lux (SD 3.23, range 16.77 - 23.90 lux) for 50% and 35.46 lux (SD 5.94, range 29.4 - 44.00 lux) for 100%.

Statistical analyses were carried out on all bat activity (the number of bat passes for all species, *P. pipistrellus*, *Myotis* spp.), feeding behaviour (buzz ratio) and mean insect counts, with standardized weather variables included as fixed factors in the GLMMs. The best models, determined by the lowest AICc values, generally included temperature (^{o}C) and wind speed (km/hr) but not mean nightly rainfall (mm). Temperature had a positive significant effect on the number of bat passes, i.e. there were more bat passes as the nightly temperature increased, whereas wind speed had a significant negative effect on the number of bat passes, i.e. there were fewer bat passes as the nightly wind speed increased. So, it was important that both variables were included as fixed effects in the model.

When considering all bat species, there were significantly more bat passes at 50% compared to 0% lighting levels, but not between 25% or 100% and 0% levels (Table 3.1). For light-opportunistic *P. pipistrellus,* the results were similar: there were significantly more passes at 50% and 100%, compared with the 0% lighting level (Table 3.1, Figure 3.2a). Conversely, higher light intensities had a negative effect on the light-averse *Myotis* spp. There were significantly fewer *Myotis* passes at 50% and 100% lighting levels, compared with the unlit treatment, but there was no significant difference between the 0% and 25% lighting levels (Table 3.1, Figure 3.2b). However, the number of bat passes on all species was not dependent on light level (Generalised linear model (GLMM): χ^2= 6.45, d.f. =1, p= 0.09). Number of *Pipistrellus pipistrellus* bat passes was also not dependent on light level (χ^2 = 70.00, d.f.= 3, p= 0.07). Whereas the number of *Myotis* spp. bat passes was dependent on light level χ^2= 13.93, d.f.= 3, p=0.003).

The insect count data also showed significantly higher insect activity at the 100% lighting level compared with the unlit treatment, but there was no difference between

0% and 25% or 50% lighting levels (Table 3.1, Figure 3.2c). There were significantly more feeding buzzes at the 25%, 50% and 100% lighting levels, compared to the unlit treatment (Table 3.1, Figure 3.2d). Mean insect count was not dependent on light level (χ^2= 5.31, d.f. =3 and p=0.15), but buzz ratio was (χ^2= 57.14, d.f. =3, p <0.001).

While there were no significant differences between intermediate light levels, i.e. 25% compared to 50% or 100%, or 50% compared to 100% (Table 3.2) for the bat activity data for any of the species or insect counts, there were significantly more feeding buzzes at 50% and 100%, compared with the 25% lighting level (Table 3.2).

Table 3.1. Results from GLMMs for the bat passes of a) all species, b) *P. pipistrellus* and c) *Myotis* spp., d) buzz ratios for all species (based on a 5% sample), and e) mean insect counts. All estimates were compared against the unlit treatment (0%). All estimates were compared against the unlit treatment (0%). Only variables included in the final model are shown, i.e. the model with the lowest AICc score. Significant results are in bold; * denotes P<0.05, ** denotes P<0.01 and *** P<0.001.

Model	Estimate	SE	Z value	P	Marginal R^2	Conditional R^2
a) All species					0.18	0.83
25%	0.17	0.16	1.06	0.23		
50%	**0.39**	**0.16**	**2.43**	**0.02***		
100%	0.29	0.16	1.81	0.07		
Temperature (ºC)	**0.47**	**0.09**	**5.08**	**<0.001*****		
Wind speed (km hr^{-1})	**-0.19**	**0.07**	**-2.57**	**0.01***		
b) *P. pipistrellus*					0.20	0.85
25%	0.13	0.17	0.77	0.44		
50%	**0.39**	**0.17**	**2.30**	**0.02***		
100%	**0.34**	**0.17**	**2.05**	**0.04***		
Temperature (ºC)	**0.53**	**0.10**	**5.45**	**<0.001*****		
Wind speed (km/hr^{-1})	**-0.25**	**0.08**	**-3.21**	**0.001****		
c) *Myotis* spp.					0.13	0.80
25%	-0.41	0.23	-1.77	0.08		
50%	**-0.83**	**0.24**	**-3.50**	**<0.001*****		
100%	**-0.74**	**0.24**	**-3.06**	**0.002*****		
Rain (mm)	-0.34	0.18	-1.84	0.07		
Wind speed (km/hr^{-1})	-0.20	0.11	-1.86	0.06		
d) Buzz ratio					0.06	0.20
25%	**0.69**	**0.22**	**3.17**	**0.001****		
50%	**1.37**	**0.22**	**6.29**	**<0.001*****		
100%	**1.19**	**0.22**	**5.41**	**<0.001*****		
Temperature (ºC)	**0.43**	**0.17**	**2.54**	**0.011***		
e) Insect counts					0.19	0.23
25%	2.69	1.42	1.89	0.06		
50%	2.73	1.42	1.92	0.06		
100%	**2.91**	**1.42**	**2.05**	**0.04***		

Table 3.2. Results of the post-hoc comparisons of the intermediate light levels applied to GLMMs for the bat passes of a) all species, b) *P. pipistrellus* and c) *Myotis* spp., d) buzz ratios for all species (based on a 5% sample) and e) mean insect counts. Lighting levels were 25 (25%), 50 (50%) and 100 (100%). Significant results are in bold; * denotes P<0.05, ** denotes P<0.01 and *** P<0.001.

Model	Estimate	SE	Z value	P
a) All species				
50-25	0.22	0.16	1.34	0.54
100-25	0.12	0.16	0.73	0.89
100-50	-0.10	0.16	-0.64	0.92
b) *P. pipistrellus*				
50-25	0.26	0.17	1.54	0.42
100-25	0.21	0.16	1.30	0.56
100-50	-0.04	0.16	-0.27	0.99
c) *Myotis* spp.				
50-25	-0.42	0.26	-1.64	0.36
100-25	-0.33	0.27	-1.25	0.59
100-50	0.09	0.27	0.33	0.99
d) Buzz ratio				
50-25	**0.68**	**0.16**	**4.19**	**< 0.001*** **
100-25	**0.50**	**0.16**	**3.12**	**0.01****
100-50	-0.18	0.16	-1.13	0.67
e) Insect counts				
50-25	0.04	0.72	0.06	1.00
100-25	0.22	0.70	0.32	0.99
100-50	0.18	0.69	0.26	0.99

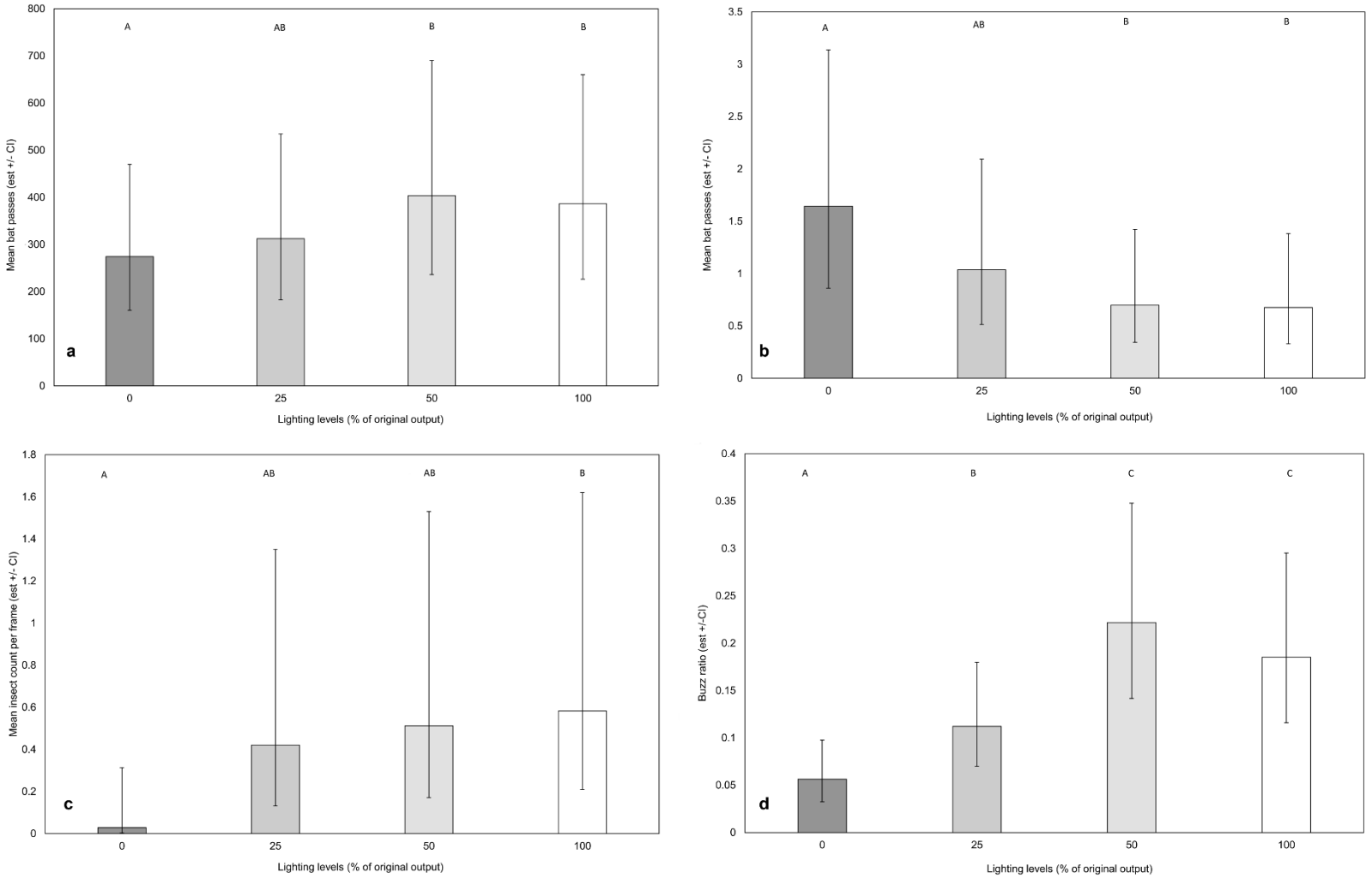

Figure 3.2. Mean predicted bat activity (number of bat passes) back-transformed across all sites (n=21) for each lighting level for a) *P. pipistrellus* and b) *Myotis spp*. c) Mean predicted insect counts back-transformed across selected sites (n=7) for each lighting level. d) Mean predicted buzz ratios back-transformed across all sites (n=21) for each lighting level. For all graphs letters identify groups that were significantly different from each other and vertical lines denote 95% confidence intervals.

3.4. Discussion

My results are broadly consistent with my hypotheses, that higher light levels (50% and 100%) increase the activity of light-opportunistic species such as *P. pipistrellus*, but reduce the activity of light-averse species such as *Myotis* spp. However, lower light levels (25%) do not affect activity levels of either light-opportunistic or light-averse species compared to the unlit treatment (0%).

The increase in the number of bat passes of the light-opportunistic *P. pipistrellus* at 50% and 100%, compared to the unlit treatment, is most probably due to a greater number of insects being attracted to the street lights at higher lighting levels. This supports the attraction-by-insects hypothesis, as opposed to the attraction-by-artificial-light hypothesis, which argues that bats are attracted to the lights for other reasons (Voigt *et al.* 2017). Foraging benefits can also be inferred from the buzz ratio data. The proportion of feeding buzzes compared to the number of bat passes was significantly higher at the 25%, 50% and 100% lighting levels than the unlit treatment. Also, there were significantly more buzzes relative to echolocation calls at the 50% and 100% lighting levels compared to the 25% level. My feeding buzz data suggest that the main benefit for bats flying close to street lights is to prey on the insects attracted to the light source. Even though the number light-opportunistic bat passes did not increase significantly at the 25% lighting level, compared to the unlit treatment, or between intermediate lighting levels (i.e. 25% and 50% or 25% and 100%), the buzz ratios increased, suggesting that these species of bats increase their feeding efficiency at street lights. This could be due in part to the reduced anti-predator behaviour of moths (Wakefield *et al.* 2015) or more probably because around street lights bats may possibly feed on large numbers of relatively small insects that have a lower energy content than larger insects.

Furthermore, there were significantly more insects at the 100% lighting level compared to the unlit treatment, and the differences between the 25% or 50% lighting levels and the unlit treatment were almost significant (Table 3.2). While there were not significantly more insects at 25% or 50% lighting levels compared to the unlit treatment, there were more feeding buzzes relative to the number of bat passes. The reason for this difference between the insect and buzz ratio data could be due to the absence of a linear relationship between the number of insects

attracted to a light source and its illuminance (Longcore *et al.* 2015). Although the lux level at the 50% lighting level (mean 20.23 lux) was double that of the 25% lighting level (mean 11.35 lux), this does not mean that double the number of insects should be attracted to the 50% lighting level. To determine the attractiveness of a light source, it is necessary to consider the spectral sensitivities of the insects (Gaston *et al.* 2012) and calculate either the square root of the ratio between the illuminance of the light source and its surrounding background (Bowden 1982) or use a function of the luminance of the light source (Stevens 1961). The difference between the insect and buzz ratio data could also be due to the smaller sample sizes for the insect counts.

Lighting level appeared to have a stronger effect at 50% than 100% for both bat activity and feeding behaviour, possibly because when the LED street lights are at 50% of their original output, there is an increase in insect numbers and hence feeding opportunities but fewer risks from potential predators. Alternatively, when light intensities increase above 50% of the original output, the illuminance may disturb bats (Lewanzik & Voigt 2017) or, at light intensities above 50%, more bats may be attracted to the higher insect numbers, and so suffer from echolocation interference from the calls of other bats. This makes it more difficult for a bat to differentiate its own returning echoes from those of conspecifics (Amichai, Blumrosen & Yovel 2015).

It is unsurprising that I found significantly fewer bat passes of *Myotis* spp. at 50% and 100% lighting levels compared to the unlit treatment (Stone, Jones & Harris 2009; Lacoeuilhe *et al.* 2014). However, it is encouraging that the low lighting level (25%) did not have a detrimental effect on the number of *Myotis* spp. passes. From a conservation perspective, this is a positive outcome as it means there is scope to work with local authorities to see if it is possible to find a light intensity that is acceptable for humans but does not adversely affect bat activity, particularly for light-averse species.

At the low lighting level (25%), as less light was distributed from the light source, it is likely that dark corridors were created that light-averse species, such as *Myotis* spp. could fly along, either as a more efficient commuting route or even to forage. However, once the street light intensities exceeded 11.35 lux, the perceived threat of

predation might become too great, significantly reducing the number of *Myotis* spp. passes near the street lights. This contrasts with an earlier study, which found that LED light intensities as low as 3.6 lux negatively affected the number of bat passes from light-averse bats such as *Myotis* spp. and *Rhinolophus hipposideros* (Stone, Jones & Harris 2012). This could be due to differences in experimental design: my study took place in suburban areas, where street lights have existed for decades, and so the bats may have adapted to the presence of artificial lights, whereas the earlier study set up their street lights in unlit areas (Stone, Jones & Harris 2012), and so the novelty of lighting may have affected the bats differently. Differences could also be because fewer *Myotis* spp. are found in suburban compared to rural areas (Figure 3.2a, b). As *Myotis* spp. are light-averse, they tend to avoid suburban areas when commuting and foraging, preferring more cluttered habitats (Norberg & Rayner 1987; Jones & Rydell 1994).

My results are consistent with findings from an earlier study which also found that light intensity had a significant positive effect on light-opportunistic species such as *P. pipistrellus*, but a significant negative effect on light-averse species such as *Myotis* spp. (Lacoeuilhe *et al.* 2014). Moreover, commuting *Myotis daubentonii* activity was not significantly reduced by exposure to dim white, green or red lights (minimum intensity of 5 lux). However, these findings were from a small-scale study at only one location, and ideally this experiment needs replication at a number of sites to determine the impact of artificial lighting on commuting *M. daubentonii* bats (Spoelstra *et al.* 2018).

Reducing the light intensities of street lights could benefit invertebrates by decreasing flight-to-light behaviour, thereby lowering the risk of mortality from exhaustion and predation, as well as preventing disruptions to biological cycles (Macgregor *et al.* 2015; de Medeiros, Barghini & Vanin 2017). To reduce the ecological impact on invertebrates, Davies *et al*. (2017) suggested that LED street lights should be dimmed to 50% of their original output (<14 lux) and adhere to a part-night lighting scheme i.e. switched off between midnight and 04:00.

In conclusion, my results support dimming as an effective strategy to mitigate the ecological impacts of street lights as it seems possible to achieve a light intensity that could benefit both light-opportunistic and light-averse species of bats (Lewanzik

& Voigt 2017), potentially realigning the balance that existed before street lighting dominated our landscapes. It is worth mentioning that ideally, installing street lights should be avoided, but this is not feasible in many areas due to safety and security reasons: in these cases, dimming street lights is a suitable mitigation strategy. I believe that further studies are required to investigate the impacts of dimming in different locations to include other light-averse species, such as *Plecotus* and *Rhinolophus* species. It would also be useful to repeat this study, using residential areas instead of A roads, where street lights are typically 5m as opposed to 10m high, and have a lower power and illuminance. It might be possible to reduce light intensities even further, while still striking the balance between maintaining biodiversity, economic benefits and human safety (Azam *et al.* 2018). Obtaining more samples could help to increase the power of these statistical analyses as light level for all species (χ^2= 6.45, d.f.= 1, p= 0.09) and *P.pipistrellus* (χ^2= 70.00, d.f.= 3, p= 0.07) did not affect the number of bat passes, even though both were very close to significance. This is particularly important for bats as the number of bat passes varies considerably over time.

Further inspection of the *Myotis* spp. bat passes reveals that the majority of these passes were at site 19 and when I re-run the statistical analysis removing this site, although the number of bat passes is still dependent on the light level (χ^2= 5.16, d.f.=3 and p=0.001). The number of passes at the 25% dimming level is now significantly lower than at 0%, which also highlights the need for more samples in this area of research.

3.5. Link to the next chapter

In this chapter I discussed how one of the strategies to mitigate the anthropogenic effects of ALAN may be beneficial to light-averse species of bats, which is important as many are of conservation concern. In the next chapter I explore spectral transmission readings of insectivorous bats, particularly to investigate if there are any differences between light-averse and light-opportunistic species. As well as LED lights being installed in many countries, other broad-spectrum light sources such as MH and FL lights are also being used. Both FL and MH lights emit some ultraviolet

(UV) wavelengths, so it is important to understand how these types of street lights may be perceived by bats.

3.6. Supplementary material

Table S3.1. The number *Pipistrellus pipistrellus* bat passes at each site over the two recording nights for the four lighting levels (0%, 25%, 50% and 100%).

Table S3.2. The number *Myotis* spp. bat passes at each site over the two recording nights for the four lighting levels (0%, 25%, 50% and 100%).

Table S3.3. Mean insect counts (SD) at each site for the four lighting levels (0%, 25%, 50% and 100%) for one recording night.

Table S3.4. The buzz ratio for all bat species at each site over the two recording nights for the four lighting levels (0%, 25%, 50% and 100%).

Figure S3.1. Mean bat activity across all sites (n=21) for each lighting level for a) *P. pipistrellus* and b) *Myotis* spp. c) Mean insect counts across selected sites (n=7) for each lighting level. D) Mean buzz ratio across all sites (n=21) for each lighting.

Table S3.1. The number of *Pipistrellus pipistrellus* bat passes at each site over the two recording nights for the four lighting levels (0%, 25%, 50% and 100%), except for sites 19, 20 and 21 (marked with an asterisk *) where only one night's data were used.

Site	No. of passes: 0%	No. of passes: 25%	No. of passes: 50%	No. of passes: 100%
1	38	2	34	51
2	323	10	46	52
3	1674	1274	1142	1173
4	293	573	385	370
5	24	34	138	31
6	531	225	50	281
7	291	135	128	84
8	1198	1533	2212	1646
9	82	117	146	78
10	58	96	63	220
11	1504	2045	1975	2123

12	167	491	1319	378
13	116	115	1072	742
14	201	60	267	171
15	1018	1695	2903	1454
16	940	1211	2024	1317
17	398	1385	598	1483
18	1673	2065	2031	2818
19*	383	266	355	400
20*	93	464	143	261
21*	88	164	97	112

Table S3.2. The number of *Myotis* spp. bat passes at each site over the two recording nights for the four lighting levels (0%, 25%, 50% and 100%), except for sites 19, 20 and 21 (marked with an asterisk *) where only one night's data were used.

Site	No. of passes: 0%	No. of passes: 25%	No. of passes: 50%	No. of passes: 100%
1	5	0	1	2
2	1	0	0	0
3	0	0	0	0
4	2	1	1	1
5	0	0	0	1
6	5	3	2	1
7	2	2	2	0
8	4	2	1	2
9	0	0	0	0
10	9	7	8	1
11	0	0	0	0
12	0	0	0	0
13	3	3	3	4
14	2	1	0	1
15	1	1	0	0
16	7	7	5	7
17	4	0	0	2
18	5	1	1	0
19*	11	20	8	8
20*	2	0	1	1
21*	5	0	0	1

Table S3.3. Mean insect counts (SD) at each site for the four lighting levels (0%, 25%, 50% and 100%) for one recording night.

Site	Mean insect count: 0%	Mean insect count: 25%	Mean insect count: 50%	Mean insect count: 100%
1	0 (0)	0.07 (0.22)	0.26 (0.36)	0.52 (0.44)
6	0.03 (0.12)	0.03 (0.12)	0.12 (0.25)	0.76 (1.17)
9	0.22 (0.46)	0.41 (0.62)	0.19 (0.47)	0.52 (1.08)
11	0 (0)	0.89 (1.20)	0.22 (0.46)	1.04 (1.40)
14	0 (0)	0.04 (0.12)	0 (0)	0.67 (1.05)
18	0 (0)	1.85 (2.69)	2.52 (3.07)	2.00 (2.21)
21	0 (0)	0.45 (0.65)	0.82 (0.92)	0.03 (0.12)
Range	0-0.22	0-1.85	0.12-1.89	0.03-2

Table S3.4. The buzz ratio for all bat species at each site over the two recording nights for the four lighting levels (0%, 25%, 50% and 100%), except for sites 19, 20 and 21 (marked with an asterisk *) where only one night's data were used.

Site	Buzz ratio: 0%	Buzz ratio: 25%	Buzz ratio: 50%	Buzz ratio: 100%
1	1.00	0.00	0.5	0.00
2	0.11	0.00	0.00	0.00
3	0.58	0.19	0.25	0.19
4	0.05	0.11	0.25	0.22
5	0.00	0.00	0.10	0.00
6	0.00	0.06	0.00	0.04
7	0.06	0.00	0.00	0.00
8	0.10	0.12	0.14	0.16
9	0.00	0.20	0.25	0.00
10	0.00	0.22	0.00	0.41
11	0.05	0.36	0.41	0.44
12	0.08	0.31	0.37	0.40
13	0.00	0.00	0.42	0.26
14	0.10	0.00	0.11	0.05
15	0.11	0.13	0.21	0.05
16	0.02	0.11	0.26	0.15
17	0.13	0.31	0.26	0.40

18	0.04	0.18	0.27	0.23
19*	0.20	0.00	0.07	0.11
20*	0.08	0.18	0.00	0.20
21*	0.00	0.10	0.00	0.00

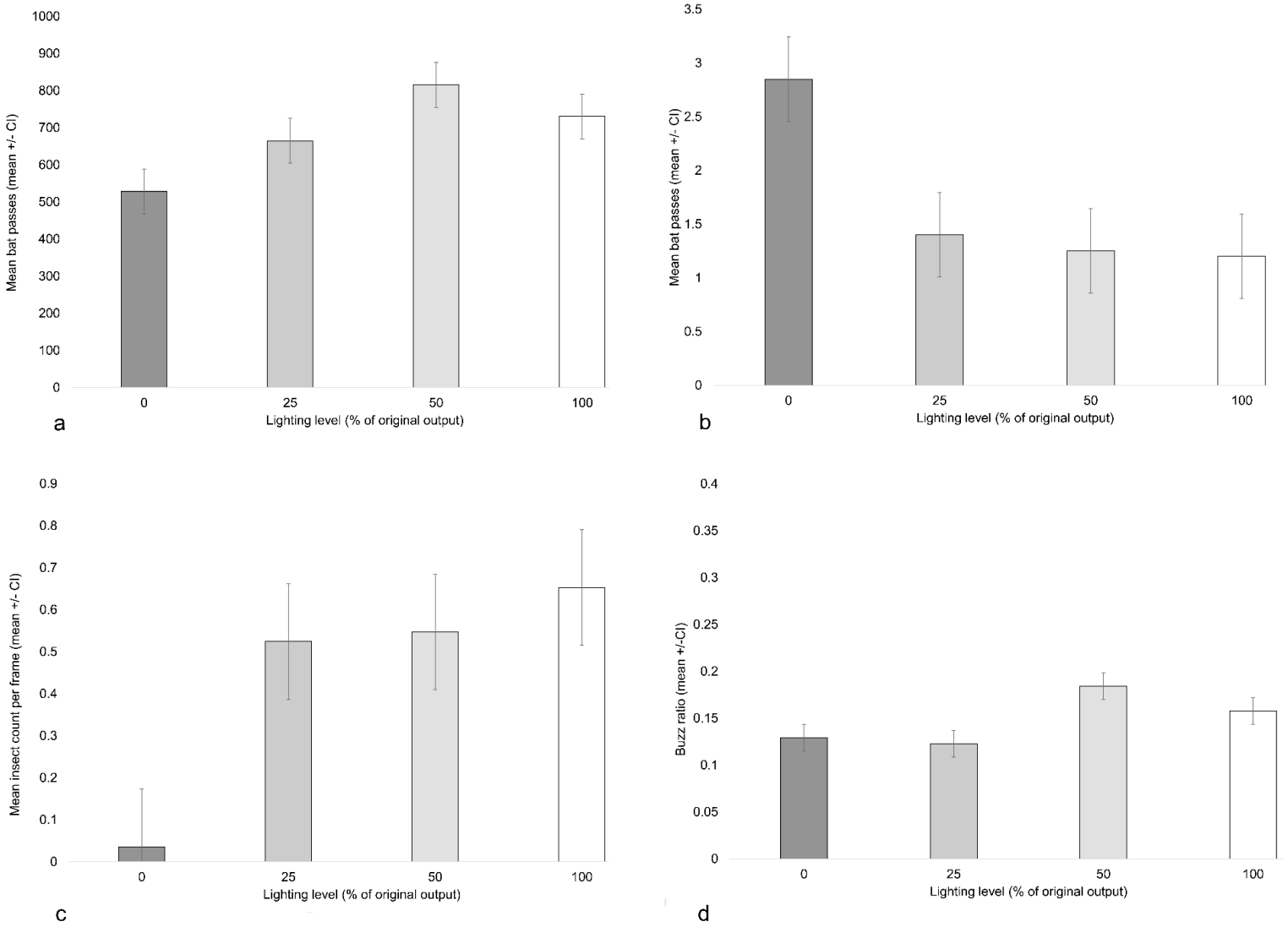

Figure S3.1. Mean bat activity across all sites (n=21) for each lighting level for a) *P. pipistrellus* and b) *Myotis* spp. c) Mean insect counts across selected sites (n=7) for each lighting level. D) Mean buzz ratio across all sites (n=21) for each lighting level.

Chapter 4: The spectral transmission of bat lenses and its implications for modern street lighting

Abstract

Echolocation is generally considered the most important sensory system for insectivorous bats, but vision can also play a role in orientation, prey detection and obstacle avoidance. Molecular, immunohistochemical, electrophysiological and behavioural studies have all demonstrated that ultraviolet (UV) vision is likely to occur in several bat lineages, although there is less information on UV vision in insectivorous bats, such as rhinolophid and vespertilionid bats found in Britain. Additionally, the spectral transmission of light through the lenses of bat eyes has been little studied. This is important when trying to assess the impact of artificial light sources on bats.

I quantified the transmission of light through the lenses of seven species of bats from two families (Rhinolophidae and Vespertilionidae). All species had highly UV transmissive lenses, with 50% transmission values ranging from 308.65 nm to 336.74 nm: There were no differences in UV-transmission between the lenses of light-opportunistic and light-averse bats. These results increase our understanding about the potential sensitivity of bats to UV wavelengths, which has important implications for street lighting strategies. Modern light-emitting diode (LED) street lights do not emit UV wavelengths, so may be less apparent to bats than metal halide (MH) and fluorescent (FL) street lights, both of which emit UV light. These differences could have behavioural consequences for bats.

4.1. Introduction

Vision is important for insectivorous bats, particularly for long-range navigation (Griffin 1970), detection of predators and prey (Suthers 1970; Bell 1985), and obstacle avoidance and orientation (Rother & Schmidt 1982; Höller & Schmidt 1996). It seems that bats integrate the information they receive from vision and echolocation

(Boonman *et al.* 2013). However in some contexts vision can impair echolocation; bats collided with objects significantly more in lit compared to dark conditions at certain points of the season (Orbach & Fenton 2010).

Vertebrates have two types of photoreceptors, rods and cones, typically used for scotopic (vision at night) and photopic (vision in day light) vision respectively (Müller, Goodman & Peichl 2007). Most mammals possess two types of cone photoreceptors that each contain a different visual pigment: either short-wavelength sensitive (SWS) pigments, which absorb ultraviolet (UV) or violet light (~360 to 440 nm), or medium-to-long-wavelength sensitive (M/LWS) visual pigments, which absorb to green/red light (~536 to 560 nm) (Yokoyama & Yokoyama 1996; Yokoyama 2000; Zhao et al. 2009). Molecular work indicates that ancestrally SWS visual pigments have their peak sensitivity or maximum spectral absorption (λ_{max}) tuned to UV wavelengths (<360 nm), but were shifted to slightly longer wavelengths (390-435 nm) in many diurnal species as part of a suite of changes that may have helped protect the retinas from the phototoxic effects of high-energy UV wavelengths (Hunt *et al.* 2007; Müller, Goodman & Peichl 2007). UV wavelengths fall between 100 and 400 nm and are commonly split into three types: UVA (315-400 nm), UVB (280-315 nm) and UVC (100-280 nm) (Cronin & Bok 2016). The atmosphere removes all of the UVC, some of the UVB, but transmits much of the UVA to the earth's surface. The use of UV light in the visual sensory systems of animals is almost entirely determined by the wavelengths that fall within the UVA range (Cronin & Bok 2016) and are the focus of this chapter.

A first step in determining if an organism has the potential for UV vision is to carry out ocular transmission measurements (Cronin & Bok 2016). The spectral sensitivity of an organism's eye depends on both the sensitivity of the photoreceptor cells and the transmission properties of the ocular tissue (Hastad, Partridge & Odeen 2009). The ocular media often act as a filter, limiting which wavelengths reach the photoreceptors in the retina (Siebeck & Marshall 2000).

It is important at this point to differentiate between UV sensitivity and UV vision. UV sensitivity is the capacity to detect wavelengths in the UV spectrum i.e. to have UV-transmissive lenses, although the SWS visual pigments do not necessarily have a λ_{max} in the UV spectrum. It is important to mention that the degree of UV sensitivity

for most animals is unknown and is likely to vary according to each species' visual system i.e. length of the outer segment, the part of the retina that contains cones and rods) (Douglas & Jeffery 2014). UV vision is the ability to differentiate UV-containing signals based on wavelength alone (Cronin & Bok 2016). Species that have UV vision are able to recognise UV wavelengths as a separate colour, as opposed to perceiving it as a different shade of blue/violet (Douglas & Jeffery 2014), just as we distinguish blue from green.

UV vision is achieved if the SWS visual pigment has a λ_{max} in the UV spectrum combined with ocular media that transmit an adequate amount of light in the UV range. However, it is also possible for an organism to be sensitive to UV wavelengths without a UV-tuned visual pigment, due to the presence of a secondary absorption peak in the UV range (cis or β-band of a longer wave visual pigment) (Hastad, Partridge & Odeen 2009). This means that if an organism has UV transmissive lenses, even without an visual pigment with a λ_{max} in the UV spectrum, it is possible for it to be sensitive to UV wavelengths (Douglas & Jeffery 2014).

Compared with other taxa, notably fish, research on vision in bats is still in its infancy. Most of what we know is from frugivorous and nectarivorous bats, with less known about insectivorous bats. Bats are adapted for a nocturnal lifestyle as they have rod-dominated eyes, but many bat species also have extensive cone populations (Müller & Peichl 2005; Müller, Goodman & Peichl 2007). Ocular transmission studies using T50 cut-off scores (the wavelength which is 50% of the maximal transmittance) show that the frugivorous pteropodid bats *Pteropus livingstonii* and *P. rodricensis* have UV transmissive lenses (T50 cut-off scores of 332-422 nm and 388 nm respectively) (Douglas & Jeffery 2014), as do the primarily nectarivorous phyllostomid bats *Carollia perspicillata* and *Glossophaga soricina* (T50 cut-off scores of ~310 nm) (Müller *et al.* 2009). Molecular and immunohistochemical studies have provided strong evidence that the nectarivorous phyllostomid bats *C. perspicillata* and *G. soricina* (Müller *et al.* 2009), the frugivorous pteropodids *Haplonycteris fischeri* and *Pteropus dasymallus formosus* (Wang *et al.* 2004), and the insectivorous vespertilionids *Myotis lucifugus* and *Myotis velifer* (Wang *et al.* 2004; Feller *et al.* 2009) have UV-tuned SWS visual pigments. Behavioural studies on bats from three families (Molossidae, Phyllostomidae and Vespertilionidae)

provide further evidence to support the existence of UV vision across many bat species (Winter, López & von Helversen 2003; Gorresen *et al.* 2015). Under scotopic light levels (light intensity 0.016 μW/cm^2) the phyllostomid bat *G. soricina* was able to detect UV light at wavelengths as short as 310nm (Winter, López & von Helversen 2003). In a choice experiment, seven wild-caught bat species from three families (Molossidae, Phyllostomidae and Vespertilionidae) chose to leave a Y-maze through an exit illuminated with reflected UV light (λ_{max}= 365 nm, light intensity 1 μW/cm^2) rather than a dark exit (Gorresen *et al.* 2015).

Molecular studies investigating the functionality of photoreceptor visual pigment genes found that SWS visual pigments have diverged across bat lineages, with some genera completely losing UV vision through the pseudogenisation of the SWS visual pigment (Zhao *et al.* 2009). It is probable that the ability to perceive UV wavelengths is linked to the type of echolocation call that the bat emits. Bats can either use low-duty cycle (LDC) or high duty-cycle (HDC) echolocation strategies (Fenton, Faure & Ratcliffe 2012). The duty cycle aspect refers to the percentage of time that a signal is produced (i.e. “on time”). LDC echolocators separate their incoming and outgoing calls based on time, i.e. they produce a call and listen to the returning echo before emitting another call (Holderied & von Helversen 2003; Holderied *et al.* 2005). In contrast, HDC echolocators separate their calls based on frequency, enabling them to emit a call and receive an echo simultaneously (Schuller 1974, 1977).

Bats from the family Vespertilionidae have functional UV-tuned SWS visual pigments. These bats emit low-duty cycle (LDC) short calls (signals are produced <25% of the total search phase call, i.e. calls are separated by long periods of silence), which are often frequency-modulated (FM) (Jones & Teeling 2006; Zhao *et al.* 2009; Fenton, Faure & Ratcliffe 2012). However, bats from the families Hipposideridae and Rhinolophidae do not have a functional SWS visual pigment; they only have an M/LWS visual pigment and so lack UV vision (Müller & Peichl 2005; Müller, Goodman & Peichl 2007; Zhao *et al.* 2009). They emit high-duty cycle (HDC) calls (signals are produced ≥25% of the total search phase call), which are dominated by a constant frequency (CF) component and longer in duration (Zhao *et al.* 2009; Fenton, Faure & Ratcliffe 2012).

This lack of UV vision could be the result of a trade-off between vision and hearing. HDC echolocators have evolved such sophisticated sensory adaptations for echolocation (Jones 2005) that it has been proposed that there is no longer a need for dichromatic vision (Zhao *et al.* 2009), which would compete for expensive neural processing and brain space. Conversely, LDC echolocating bats may use vision to enhance information collected acoustically (Zhao *et al.* 2009). This is supported by reduced visual brain structures and eye size compared with auditory structures in HDC bats (Baron, Stephan & Frahm 1996; Thiagavel *et al.* 2017), and increased rate of evolution of the Slc26a5 gene, which encodes Prestin; a protein in the outer hair cells involved in echolocation (Liu *et al.* 2014). Immunohistochemical and behavioural studies have also highlighted this vision/echolocation trade-off; the LDC echolocator *Scotophilus kuhlii*, which has UV-tuned SWS visual pigments, reacted to UV light by exhibiting conditioned reflexes such as body crouching and wing retracting. In contrast, the HDC echolocator *Hipposideros armiger* does not have a UV-tuned SWS visual pigment and did not show any visible responses to exposure to UV light (Xuan *et al.* 2012a, b).

The type of echolocation calls a bat produces also influences vision in dim light, which under scotopic conditions relies on the initiation of the rod visual pigment rhodopsin (Rh1). A recent study showed that although there were no differences in the peak spectral sensitivities (λ_{max}) of Rh1 for three bat species (498.0 nm, 496.4 nm and 500.0 nm) for the HDC echolocator *Rhinolophus ferrumequinum*, LDC echolocator *Myotis lucifugus* and non-echolocating *Pteropus alecto* respectively. There were however differences in the rhodopsin kinetics, the stability of the rhodopsin intermediate state (metarhodopsin II). The decay rates of the light-activated state of the LDC echolocator *M. lucifugus* was significantly slower compared to the HDC echolocator *R. ferrumequinum*, indicating that HDC and LDC echolocating bats rely on vision and hearing differently during orientation and foraging (Gutierrez *et al.* 2018a).

Loss of UV vision resulting from a pseudogenised SWS visual pigment is also apparent in non-HDC echolocating bats, including bats from the families Megadermatidae and Mormoopidae, as well as vampire bats from the sub-family Desmodontinae that rely on senses such as thermoreception and olfaction to locate

large animal prey in the dark (Kries *et al.* 2018; Simões *et al.* 2018). The absence of UV vision in non-echolocating bats is linked to roost lighting levels (Müller, Goodman & Peichl 2007). An immunohistochemical and behavioural study carried out in photopic light levels found that tree-roosting bat species, exposed to higher light levels, retained cone-based UV vision, whereas cave-roosting bat species did not (Xuan *et al.* 2012a, b). However, there are exceptions, including a functional SWS gene in a cave-roosting species *Lissonycteris angolensis* (Simões *et al.* 2018).

Clade model analyses have also demonstrated that the environment in which bats forage may be important for explaining bat vision (Gutierrez *et al.* 2018b). Divergent selection occurs more often bat species that forage in cluttered environments, compared to those species that forage in more open habitats or along the edge of vegetation. In cluttered environments, such as forests, where there tends to be a greater proportion of medium-to-long wavelengths compared to short wavelengths, there may be insufficient light to activate the SWS visual pigment, possibly leading to the relaxation of constraint upon the visual pigment. This phenomenon has been identified in nocturnal lemurs that live in areas of high vegetation (Veilleux, Louis & Bolnick 2013), where many have a SWS pseudogene, as well as some bat species (Zhao *et al.* 2009; Dong *et al.* 2017). Bats that emerge relatively soon after sunset, when there is a high proportion of short wavelengths, may also benefit from having UV vision as it could increase the amount of photons captured and so help when catching insects (Müller *et al.* 2009; Gutierrez *et al.* 2018b). Spiders that inhabit darker, shaded forested habitats have higher T50 cut-off scores (i.e. ocular media transmitted less UV light) than spiders that lived in habitats that received more light (Hu *et al.* 2012).

Insectivorous bats are typically most active at dusk and dawn and so are normally only exposed to low intensity light, where their eyes operate more efficiently than under brightly lit conditions (Boonman *et al.* 2013; Gorresen *et al.* 2015). Many bats are also influenced by artificial light at night (ALAN), especially that emitted by street lights (Gaston *et al.* 2012). Street lights emit a range of spectral emissions (Elvidge *et al.* 2010). Globally, there is a current trend to switch from narrow spectrum street lights, such as LPS and HPS lights, to broad-spectrum “white” lights such as MH, FL and LED lights (De Almeida *et al.* 2014; Rowse, Harris & Jones 2016; Wakefield *et*

al. 2017). While these broad-spectrum street lights are often marketed as “green or environmentally friendly” technologies (Stone, Jones & Harris 2012; Wakefield *et al.* 2017), these terms are potentially misleading as they do not consider the ecological consequences of these broad-spectrum light sources. FL and MH street lights, for example, emit very short wavelengths into the UV spectrum (Elvidge *et al.* 2010). UV wavelengths are highly attractive to many insects (Cowan & Gries 2009; Eisenbeis 2006) and therefore to many bats that prey on them (Blake *et al.* 1994), and so have the potential for far-reaching effects on a range of organisms (Gaston *et al.* 2012).

ALAN has a variable effect on insectivorous bats: some are light-opportunistic and prey on the insects that are attracted to the street lights (Blake *et al.* 1994), whereas others are light-averse and avoid street lights (Voigt *et al.* 2018). In contrast to light-opportunistic bats that tend to emerge earlier and forage in relatively open habitats, often close to artificial light sources (Rydell 1992; Blake *et al.* 1994; Jones & Rydell 1994, Lacoeuilhe *et al.* 2014), light-averse species emerge later, after sunset, and commute along linear features in cluttered habitats, foraging in darker areas (Stone, Jones & Harris 2012). These different foraging and commuting behaviours could be associated with differences in the ocular transmissions of these two groups.

My aim was to determine the spectral transmission of the lenses of a number of British bat species. I tested the following two hypotheses:

1. There would be differences in the UV transmission between light-opportunistic and light-averse bat species. I hypothesised that light-opportunistic bat species would have more UV transmissive lenses than light-averse species as they are exposed to more light while commuting and foraging.

2. The lenses of rhinolophid bats are less UV-transmissive than vespertilionid bats because, unlike rhinolophids, vespertilionid bats have a UV-tuned SWS visual pigment and so are more likely to benefit from lenses that transmit more UV wavelengths.

4.2. Methods

4.2.1. Experimental set-up

All bats used in this study were carcasses donated by bat carers, veterinarians or rescue centres: they all died naturally or were euthanized owing to injury or illness. Bats were freeze-dried within 24 hours of death, which ensured excellent preservation of the eyes. There is no difference between the spectral transmission of fresh and frozen lenses (Douglas & Jeffery 2014). Bats cadavers remained frozen until spectral transmission measurements were taken.

The spectral transmission of the lenses of 25 juvenile and adult bats belonging to seven species (Table 4.1) from two families (Rhinolophidae and Vespertilionidae) were measured. Only lenses were measured, as the small size of the eyes of these bat species meant that it was too difficult to remove and measure the other ocular media (cornea, aqueous or vitreous humours). Lenses were removed from the eyes and cleaned using phosphate-buffered saline (PBS). All lenses were measured within 30 minutes of being removed from the eye to avoid tissue degradation (Douglas & McGuigan 1989). Only one measurement was taken per individual bat, randomly selecting if the lens was taken from the right or left eye.

Lens spectral transmission measurements were made using a QE6500 spectrophotometer (Ocean Optics, Dunedin, Florida 33777, USA). The lenses were directly mounted onto the core of the optical fibre (400 µm, Ocean Optics), which was then completely enclosed in an integrating sphere to ensure that none of the light directed through the lens was lost due to scattering and refraction. The 400 µm optical fibre upon which the bat lens was placed was attached to a deuterium lamp on a DH-2000 UV-VIS-NIR light source. To ensure that the light source was at full intensity, it was given 20 minutes to warm up and stabilize prior to taking any measurements. The integrating sphere was attached to a QE6500 spectrophotometer (QE65000, Ocean Optics) by another optical fibre (600 µm; Ocean Optics). SpectraSuite software (Ocean Optics) was used to collect digital measurements. Prior to each transmission recording, the spectrophotometer was calibrated with a light and dark measurement. The white reference was taken without a lens on the fibre and a dark background by removing the cable that was attached

to the spectrophotometer. All transmission recordings were taken with an integration time of 6000 ms and three-point boxcar smoothing.

All transmission measurements were normalised between 300 and 800 nm and the T50 cut-off score (the wavelength which is 50% of the maximal transmittance) determined. In contrast to absolute transmission readings, the T50 cut-off score is a robust metric to compare UV transmission between the different species because it is not affected by variance resulting from measurement error (Douglas & McGuigan 1989). To mitigate any ambiguity from the T50 cut-off scores, i.e. if two species had very similar T50 cut-off scores but their spectral curves followed different slopes (i.e. steep versus gradual cut-offs), I also calculated the % UVA transmitted. The % UVA transmitted measures the proportion of light between 315 and 400 nm that is transmitted by the lens following the method used in Douglas & Jeffery (2014).

4.2.2. Statistical analyses

All statistical analyses were carried out in R studio using R version 3.3.3 (R Development Core Team, 2017). It was not possible to compare the T50 cut-off scores of the vespertilionid versus rhinolophid bats statistically due to insufficient sample size, so I compared the T50 cut-off scores of light-opportunistic and light-averse species (Table 4.1). As these data were not normally distributed, I used permutation tests, based on Monte-Carlo resampling using the coin package (Hothorn *et al.* 2008) to determine if there was a difference in the T50 cut-off scores between light-opportunistic and light-averse species.

I also compared the proportion of UVA transmitted by the lens (% UVA transmitted) between light-opportunistic and light-averse bats. These data were normally distributed, so I used an independent samples *t*-test.

4.3. Results

Due to the opportunistic nature of this study, the number of samples for each species was dependent on which species came into care and subsequently died. While most of my samples were from *P. pipistrellus* (40%), I was able to get a range of both

light-opportunistic and light-averse bats as categorised in Voigt *et al.* (2018) (Table 4.1).

Table 4.1. Summary of results of bat lens spectral transmission (see supplementary material, Table S4.1 for the lens transmittance measurements of all 25 bats). % UVA transmitted measures the amount of light between 315 and 400 nm that is transmitted by the lens. T50 cut-off score is the wavelength which transmits 50% of the light. Measurements for lens diameter were taken from both eyes. It was not possible to measure the diameter of all lenses as some had degraded after completion of the spectral transmission measurement procedure**.**

Family	Species	Light-opportunistic or averse	No. of lenses measured	%UVA transmitted Mean (SD)	T50 cut-off score (nm) (mean, SD)	Lens diameter (mm) (mean, SD)
Vespertilionidae	*Eptesicus serotinus*	Opportunistic	1	72.41	313.07	1.16
Vespertilionidae	*Myotis mystacinus*	Averse	2	60.86 (16.31)	314.28 (4.54)	-
Vespertilionidae	*Myotis nattereri*	Averse	3	69.97 (1.05)	313.34 (2.28)	1.06 (0.10
Vespertilionidae	*Pipistrellus pipistrellus*	Opportunistic	10	66.00 (7.87)	314.72 (7.90)	0.76 (0.21)
Vespertilionidae	*Pipistrellus pygmaeus*	Opportunistic	1	74.59	309.86	-
Vespertilionidae	*Plecotus auritus*	Averse	6	62.85 (14.91)	321.97 (11.39)	1.45 (0.07)
Rhinolophidae	*Rhinolophus ferrumequinum*	Averse	2	54.40 (4.08)	326.31 (13.60)	0.91 *

* Measured the lens diameter of one *R. ferrumequinum* bat.

The T50 cut-off scores for all bat species were on average 316.92 nm (range 308.65 - 336.74 nm). The amount of UV light transmitted did not vary between light-opportunistic and light-averse bats (Z=-1.48, p= 0.14). Furthermore, there was little difference between the vespertilionid (mean 316.11 nm, SD 8.38 nm) and rhinolophid bats (326.31 nm, SD 13.60 nm). Due to the low sample size, this difference was not tested for statistical significance.

At 350 nm, bat lenses transmitted on average 80.88% of light and the average % UVA transmittance was 64.98% (range 44.85 - 82.43%). There was no difference in the proportion of UVA transmitted by the lens between light-opportunistic and light-averse bats (t = 1.10, df = 20.71, p = 0.29). Both the results from the T50 cut-off scores and % UVA transmitted results indicate that rhinolophid and vespertilionid bats have highly UV transmissive lenses and that there was no difference in UV transmittance between light-opportunistic and light-averse bats.

Generally, all bat species had smooth transmission curves that rapidly decreased at short wavelengths (Figure 4.1 for the spectral transmission curves of representative lenses and Figure 4.2 for spectral transmission curves of all species). The lenses from bat species could be categorised as type 1 lenses, which contain a steep drop in the curve on the short wavelength arm, with sharp cut-off at UV wavelengths between 315 and 354 nm (Douglas & McGuigan 1989).

In addition, curves have been included from a species of frugivorous bat, the Rodrigues flying fox (*Pteropus rodricensis*) and the southern flying squirrel (*Glaucomys volans*) to provide comparisons with the transmittance curves of the lenses from bat species. The lenses of the insectivorous bat species in my study were compared to these two mammals because they fly or glide and are nocturnal.

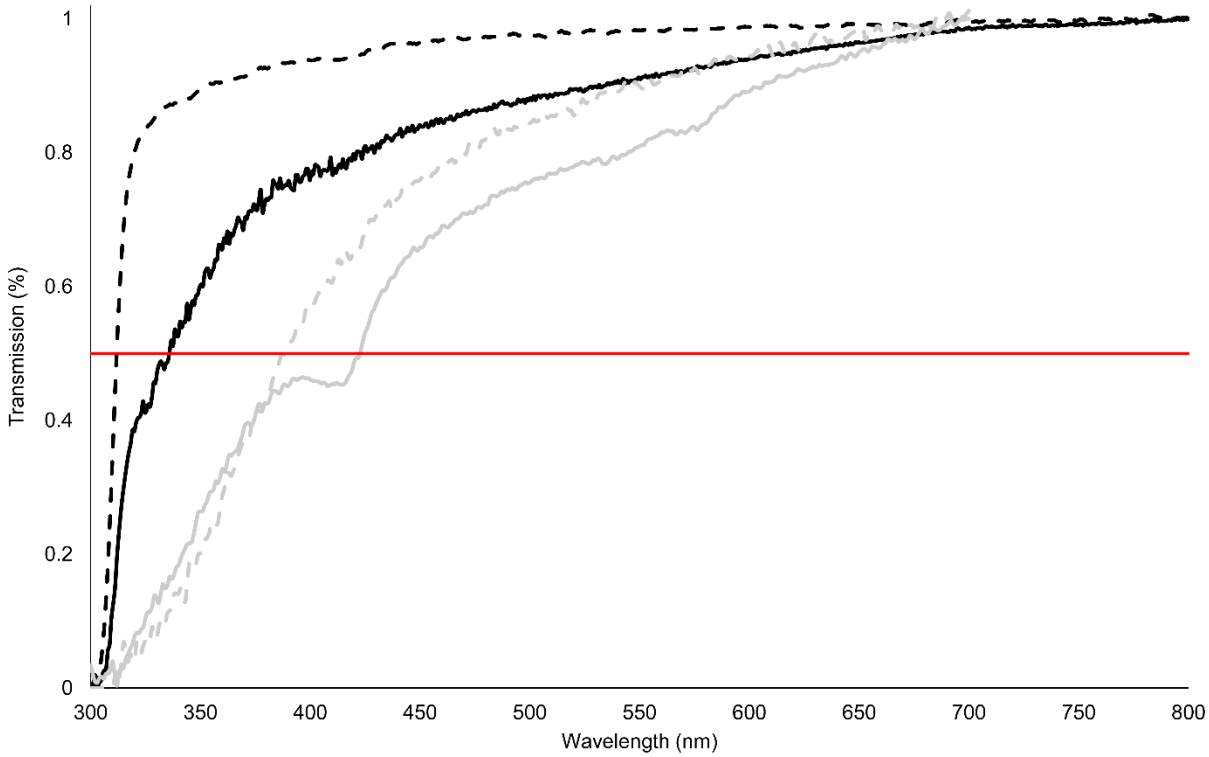

Figure 4.1. Lens spectral transmission curves for bats in this study. From left to right, the curves are *P. auritus* (spectral transmissive curve representative of vespertilionid bats) (black dashed line) and *R. ferrumequinum* (black solid line), *P. rodricensis* (grey dashed line), *G. volans* (grey solid line) (these additional transmission curves are courtesy of Ron Douglas). The red line denotes the 50% transmittance cut-off score.

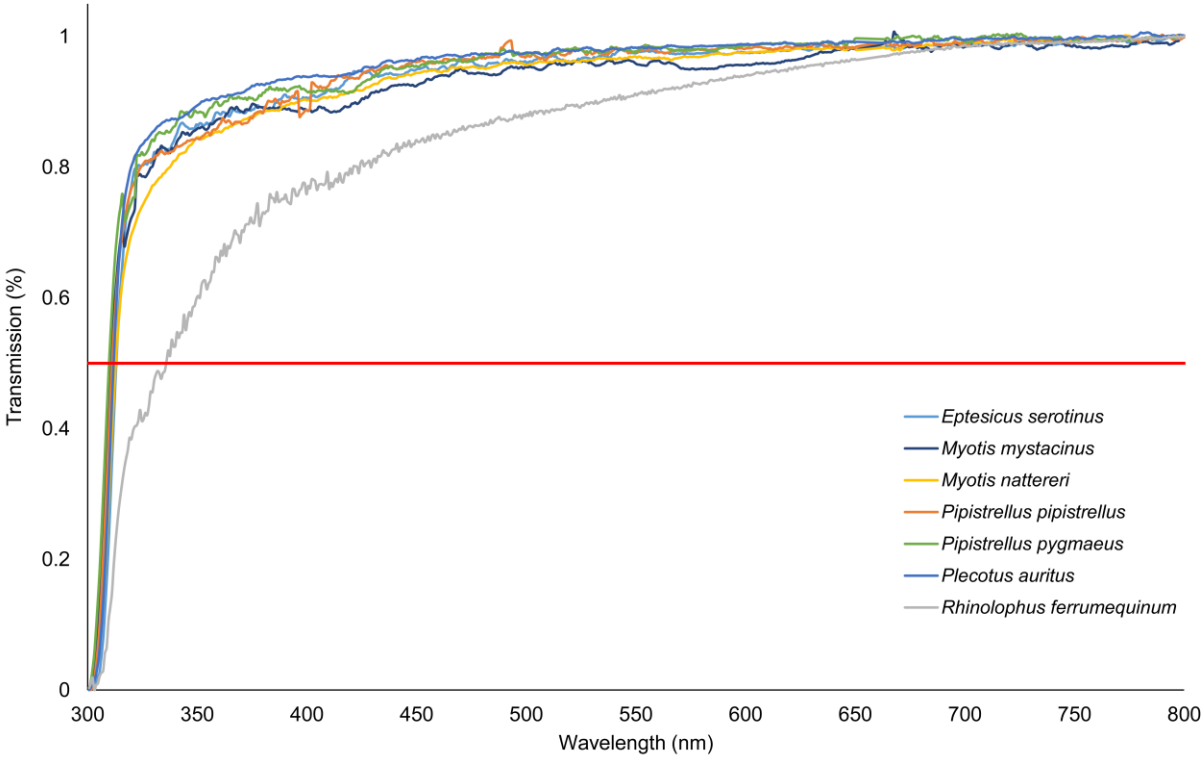

Figure 4.2. Representative spectral transmission curves of all lenses for the seven bat species measured in this study (Supplementary material, Table S4.1 for the spectral transmisson readings of all 25 bats).

The curves for lenses from both the frugivorous bat *Pteropus rodricensis* and the flying squirrel *Glaucomys volans* are shallower, with more gradual cut-offs than the curves from the lenses of the insectivorous bats (Figure 4.1, T50 cut-off scores of 388 nm and 423 nm respectively). The results highlight how much further into UV wavelengths insectivorous bat lenses transmit compared with other mammals with similar lifestyles.

4.4. Discussion

Rhinolophid and vespertilionid bats possess UV-transmissive lenses and transmit high amounts of UV (T50 cut-off scores 308.65 – 336.74 nm) and there was no difference in either the T50 cut-off scores or the proportion of UVA wavelengths transmitted by the lens between light-opportunistic and light-averse bats. Although not significantly different, on average light-opportunistic bats tended to show slightly

lower T50 cut-off scores (mean 314.17 nm, SD 7.29 nm) and slightly higher % UVA transmitted (mean 67.25%, SD 7.71%), than light-averse bats (T50 cut-off score: mean 320.16 nm, SD 9.93 nm and % UVA transmitted: mean 62.10%, SD 12.07%). Although the sample size was biased towards two species *P. pipistrellus* and *P. auritus*, as there was little variation in the T50 cut-off scores between the vespertilionid bats (Figure 4.2), this is unlikely to have an effect on the overall results. While light-opportunistic bats tend to emerge earlier after sunset, forage in more open habitats and take advantage of increased insect abundances around artificial lights compared to light-averse bats, at a landscape level, light-opportunistic bats seem to avoid ALAN (Hale *et al.* 2015; Azam *et al.* 2016; Pauwels *et al.* 2019). Therefore, the similarity of lens transmission scores between light-opportunistic and light-averse bat species could be because their foraging behaviours are not as distinct as other taxa (Hu *et al.* 2012).

The lenses of British bats can be classified as type 1 lenses as they present steep curves, with a sharp cut off. Type 1 lenses are unlikely to contain a specialised absorption pigment and so will transmit wavelengths down to 300 nm, the biological limit for transmission (Douglas & McGuigan 1989). If wavelengths below 300 nm transmit across ocular media, the radiation would break down nucleic acid and protein structures in the eye (Douglas & Jeffery 2014). Fish with type 1 lenses tend to be nocturnal or bottom feeders, so are exposed to relatively little light. Many fish species with type 1 lenses rely on sensory systems in addition to vision for feeding (Douglas & McGuigan 1989). This is similar to insectivorous bats that utilise echolocation to a greater extent than vision to orientate and catch prey (Griffin 1958; Altringham & Fenton 2003).

The presence of UV transmitting lenses in all the species I examined was in agreement with previous ocular media transmission studies of frugivorous (Douglas & Jeffery 2014) and nectarivorous bats (Müller *et al.* 2009). Nocturnal taxa such as owls also seem to have UV transmissive lenses: the northern-long eared owl (*Asio otus*), tawny owl (*Strix aluco*) and Boreal (Tengmalm's) owl (*Aegolius funereus*) have T50 cut-off scores of 351 nm, 353 nm and 335 nm respectively (Lind *et al.* 2014). However, this does not seem to be the case for all nocturnal taxa: the flying squirrel

Glaucomys volans has UV absorbing lenses, with a T50 cut-off score of 423 nm (Douglas & Jeffery 2014) (Figure 4.1).

Having UV transmissive lenses does not mean that an organism has UV vision. Even with UV transmissive lenses, UV vision can only be achieved if SWS visual pigments have a λ_{max} in the UV wavelengths, and confirmation of UV vision requires evidence from microspectrophotometry (MSP), immunohistochemical, electrophysiological and/or behavioural studies (Losey *et al.* 1999; Siebeck & Marshall 2001). However molecular work on *M. velifer* (Wang *et al.* 2004) and *M. lucifugus* (Feller *et al.* 2009) demonstrate the likelihood of UV-tuned SWS visual pigments and the behavioural study from seven species of insectivorous bats (Gorresen *et al.* 2015), plus the lens transmission readings from my study, are strong evidence that insectivorous vespertilionid bats not only have UV sensitivity, but also UV vision, i.e. the ability to distinguish UV from other wavelengths.

UV vision could benefit bats in several ways, including increasing the amount of light entering a bat's eye, which is important as bats generally inhabit dimly lit conditions, where visual sensitivity is more important than visual acuity (Job & Bellwood 2007; Douglas & Jeffery 2014). UV vision could also help insectivorous bats catch prey. There is a higher proportion of UV wavelengths than longer visible wavelengths during dusk and dawn (Lythgoe 1979; Hut, Scheper & Daan 2000). As approximately 80% of nocturnal Lepidoptera wings reflect UV light, this might make it easier for insectivorous bats to catch prey successfully (Lyytinen, Lindstrom & Mappes 2004; Zhao *et al.* 2009). Similarly, fish that prey on plankton take advantage of the contrast between the UV rich water and the small UV absorbing and sometimes reflecting prey items (Douglas, Partridge & Marshall 1998; Loew *et al.* 1993; Siebeck & Marshall 2000; Johnsen & Widder 2001). Other possible benefits of UV vision include entraining circadian rhythms (Jacobs 1992) and orienting using polarized skylight (Greif *et al.* 2014).

The potential benefits of UV vision must outweigh any possible costs of having UV transmissive ocular media, namely photochemical damage to the retina (Zigman 1971; Douglas & McGuigan 1989; Siebeck & Marshall 2000) and reduced visual acuity (Douglas & Marshall 1999). As the optical media of many nocturnal and crepuscular species transmit UV wavelengths, they experience increased Rayleigh

scattering and chromatic aberration, both of which can reduce image quality and resolution by adding noise to the main image signal (Walls 1931; Douglas & Jeffery 2014). However, chromatic aberration is less likely to be a problem since insectivorous bats have small eyes (mean eyeball axial length 2.09 mm, SD 0.86 mm (Eklöf 2003; Winter, López & von Helversen 2003). Furthermore, as insectivorous bats are most active during dimly lit periods (i.e. dusk and dawn), visual sensitivity is more important than visual acuity (Douglas & Jeffery 2014). However, it is also possible that UV sensitivity offers no advantage to insectivorous bats because there is no selective pressure to shift their SWS visual pigments from UV tuned to violet/blue tuned, as they are not continually exposed to UV radiation (Müller *et al.* 2009; Douglas & Jeffery 2014).

It seems that UV transmitting lenses are quite widespread in mammals; Douglas & Jeffery (2014) measured the UV transmittance of lenses from 38 species and found that 19 of them (50%) had UV transmissive lenses. This included a range of diurnal and nocturnal species such as the hedgehog (*Erinaceus europeus*), Rodrigues flying fox (*Pteropus rodricensis*), cat (*Felis catus*) and reindeer (*Rangifer tarandus*). These species might be UV-sensitive even without a UV-tuned visual pigment.

Unfortunately, due to the opportunistic nature of my study I was unable to compare ocular transmission values between bat species from the families Rhinolophidae and Vespertilionidae and so was unable to explore the differences between LDC and HDC echolocators (Zhao *et al.* 2009). However, these data suggest that rhinolophids have UV transmissive lenses (T50 cut-off scores, mean 326.31 nm, SD 13.60 nm and % UVA transmitted, mean 54.40%, SD 4.08%). So, while rhinolophids will not have true UV vision as they do not have an UV-tuned SWS visual pigment, it is possible that they will have some UV sensitivity from a secondary absorption peak (β-band) in the UV part of the spectrum of their M/LWS visual pigment or rod visual pigment. It is therefore possible that rhinolophid bats are less affected by UV wavelengths than vesper bats as less UV emissions are absorbed by the visual pigments of rhinolophid bats.

It is important to understand the range of wavelengths that bats are sensitive to as this has implications for street lighting guidelines. While there is a trend across Britain and much of Europe towards switching old lighting stock to LED lights

(Rowse, Harris & Jones 2016), broad-spectrum lighting technologies, such as MH and FL lights, are still used (Stone *et al.* 2015). These emissions could also contribute to skyglow as shorter wavelengths, such as UV emissions are more prone to Rayleigh scattering than longer wavelengths. This means that these UV emissions could affect bats at a broader scale, i.e. at a landscape-level, rather than local-level effects at a single light source. This could be advantageous for bats, particularly light-opportunistic bats as could aid predation.

Most studies to date on the effects of ALAN on bat activity have focused on how different spectral emissions affect insect attraction, which then has an impact on bat activity. While this may be true for light-opportunistic species, few studies consider how street lights with different spectral emissions could also affect the vision of bats, which may be of greater importance for light-averse bats, many of which are of conservation concern (Jones, Purvis & Gittleman 2003; Lewanzik & Voigt 2017). When street lights were switched from high-pressure mercury vapour (HPMV) lamps to LED lights in Germany, there were significantly more bat passes of the light-averse *Myotis* spp. One possible explanation could be that removing the UV component made the street lights less visually disturbing to light-averse bats (Lewanzik & Voigt 2017). While light-averse bats do not feed around street lights, reducing the UV component of street lights could reduce the amount of time light-averse bats spend commuting and foraging if they are more likely to fly in close proximity to the lights. This could have a positive impact on a bat's fitness, which is important since bats are slow-reproducing (Dietz 2009) and often of conservation concern.

Given that both light-averse vesper bats and light-averse rhinolophid species have UV transmissive lenses and that it is only vesper bats have UV-tuned SWS visual pigments, demonstrates that UV vision cannot be a selective advantage. Instead UV-emitting light sources could benefit light-opportunistic bats by helping these bats to catch prey, possibly further disadvantaging light-averse bats. This is because short wavelengths, such as UV-emissions are highly attractive to a number of nocturnal insects, and so these light sources are likely to draw more insects away from their typical foraging areas. Over time, this vacuum effect means that there will be fewer prey items for light-averse bats.

My results highlight the prevalence of UV-transmissive lenses across British bats, and studies on the effects of ALAN on insect (Wakefield *et al.* 2017) and bat activity (Stone *et al.* 2015; Rowse, Harris & Jones 2016; Lewanzik & Voigt 2017) indicate that, when switching to broad-spectrum technologies, LED lights should be installed rather than MH or FL street lights. While LED lights do not mitigate all the ecological effects of ALAN, as the presence of any artificial light has a number of effects on a range of organisms (Gaston *et al.* 2012; Stone, Jones & Harris 2009, 2012; Wakefield *et al.* 2017), they seem to be the most environmentally and ecologically friendly of all the broad-spectrum street lights. This is mainly because LED lights do not have UV emissions, which appear to be the most disruptive to a range of taxa (Lewanzik & Voigt 2017; Wakefield *et al.* 2017).

4.5. Link to the next chapter

In this chapter I discussed how UV sensitivity may be widespread across insectivorous bats, further supporting the case for using LED street lights as opposed to cheaper broad-spectrum alternatives, such as FL and MH lights. In the next chapter I will discuss the outcomes of all three data chapters, as well as highlighting future research directions for the effect of ALAN on bats.

4.6. Supplementary material

Table S4.1. The spectral transmission of the lenses of 25 individuals from seven bat species.

Table S4.1. The spectral transmission of the lenses of 25 individuals from seven bat species.

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
λ																										
300.62		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
301.42		0.00	0.00	0.03	0.00	0.00	0.00	0.02	0.05	0.02	0.01	0.00	0.00	0.00	0.10	0.01	0.09	0.01	0.00	0.03	0.00	0.00	0.01	0.01	0.04	0.01
302.22		0.00	0.00	0.06	0.01	0.00	0.01	0.01	0.09	0.03	0.01	0.01	0.08	0.03	0.03	0.02	0.14	0.02	0.02	0.00	0.01	0.00	0.00	0.03	0.08	0.02
303.03		0.00	0.01	0.09	0.01	0.01	0.01	0.02	0.14	0.06	0.01	0.02	0.02	0.10	0.05	0.03	0.05	0.00	0.03	0.06	0.02	0.01	0.00	0.06	0.00	0.04
303.83		0.01	0.02	0.12	0.02	0.01	0.02	0.03	0.20	0.10	0.02	0.04	0.04	0.01	0.05	0.04	0.11	0.01	0.05	0.00	0.03	0.01	0.01	0.09	0.06	0.06
304.64		0.02	0.01	0.15	0.03	0.02	0.04	0.02	0.26	0.14	0.04	0.07	0.04	0.09	0.06	0.06	0.00	0.01	0.07	0.03	0.04	0.02	0.02	0.14	0.16	0.09
305.44		0.03	0.02	0.18	0.05	0.03	0.06	0.02	0.32	0.18	0.06	0.10	0.08	0.03	0.13	0.08	0.10	0.02	0.10	0.06	0.07	0.03	0.03	0.18	0.03	0.13
306.24		0.05	0.02	0.20	0.08	0.04	0.09	0.04	0.37	0.24	0.09	0.15	0.03	0.16	0.15	0.11	0.05	0.03	0.12	0.12	0.10	0.05	0.05	0.24	0.12	0.18
307.05		0.08	0.04	0.23	0.11	0.06	0.13	0.07	0.42	0.30	0.13	0.20	0.09	0.17	0.12	0.14	0.18	0.03	0.15	0.11	0.13	0.08	0.08	0.30	0.14	0.24
307.85		0.12	0.04	0.25	0.16	0.08	0.18	0.09	0.47	0.36	0.17	0.26	0.07	0.24	0.04	0.18	0.15	0.06	0.18	0.22	0.18	0.11	0.12	0.36	0.17	0.29
308.65		0.17	0.04	0.27	0.21	0.10	0.24	0.11	0.51	0.42	0.22	0.32	0.20	0.25	0.19	0.23	0.18	0.06	0.22	0.23	0.23	0.14	0.17	0.42	0.17	0.35
309.46		0.23	0.05	0.29	0.27	0.13	0.31	0.15	0.55	0.48	0.27	0.38	0.24	0.20	0.17	0.28	0.29	0.10	0.25	0.26	0.28	0.19	0.22	0.48	0.28	0.41
310.26		0.29	0.08	0.30	0.33	0.17	0.37	0.19	0.59	0.54	0.33	0.44	0.33	0.26	0.31	0.33	0.39	0.13	0.29	0.35	0.34	0.23	0.28	0.53	0.22	0.47
311.07		0.37	0.10	0.32	0.40	0.20	0.44	0.22	0.61	0.59	0.39	0.50	0.38	0.30	0.22	0.39	0.48	0.15	0.32	0.44	0.39	0.28	0.35	0.58	0.34	0.52
311.87		0.44	0.12	0.33	0.46	0.24	0.50	0.22	0.64	0.63	0.45	0.54	0.48	0.38	0.29	0.44	0.50	0.19	0.35	0.57	0.44	0.33	0.41	0.63	0.39	0.57
312.67		0.51	0.15	0.35	0.52	0.27	0.56	0.27	0.66	0.67	0.50	0.59	0.48	0.39	0.38	0.49	0.52	0.22	0.38	0.55	0.49	0.37	0.47	0.67	0.38	0.61
313.47		0.57	0.18	0.36	0.58	0.30	0.61	0.30	0.68	0.70	0.54	0.63	0.65	0.41	0.40	0.53	0.47	0.25	0.40	0.46	0.53	0.41	0.53	0.70	0.46	0.64
314.28		0.64	0.22	0.37	0.62	0.33	0.66	0.33	0.70	0.73	0.58	0.66	0.56	0.50	0.43	0.57	0.56	0.28	0.42	0.59	0.57	0.45	0.58	0.72	0.43	0.67
315.08		0.69	0.26	0.38	0.66	0.35	0.69	0.34	0.72	0.75	0.62	0.68	0.56	0.49	0.46	0.60	0.65	0.30	0.44	0.63	0.60	0.48	0.62	0.74	0.46	0.69
315.88		0.74	0.29	0.39	0.69	0.38	0.72	0.36	0.73	0.76	0.65	0.70	0.55	0.48	0.42	0.64	0.62	0.32	0.46	0.65	0.63	0.51	0.65	0.76	0.53	0.71

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
316.69		0.72	0.24	0.39	0.72	0.39	0.75	0.34	0.74	0.77	0.67	0.72	0.65	0.51	0.46	0.67	0.61	0.34	0.51	0.70	0.65	0.54	0.69	0.72	0.40	0.68
317.49		0.74	0.28	0.40	0.73	0.41	0.76	0.37	0.74	0.78	0.69	0.73	0.64	0.54	0.56	0.68	0.62	0.35	0.52	0.71	0.66	0.56	0.72	0.72	0.51	0.69
318.29		0.77	0.30	0.40	0.75	0.42	0.78	0.37	0.75	0.78	0.70	0.75	0.67	0.49	0.52	0.70	0.66	0.37	0.53	0.67	0.67	0.58	0.74	0.73	0.53	0.70
319.10		0.80	0.33	0.40	0.77	0.43	0.79	0.39	0.76	0.79	0.71	0.76	0.50	0.58	0.69	0.72	0.62	0.39	0.55	0.74	0.69	0.59	0.76	0.74	0.94	0.71
319.90		0.81	0.35	0.41	0.78	0.44	0.80	0.40	0.76	0.78	0.71	0.77	0.62	0.54	0.60	0.73	0.64	0.38	0.56	0.69	0.70	0.61	0.77	0.75	0.46	0.72
320.70		0.82	0.37	0.42	0.79	0.45	0.81	0.40	0.77	0.79	0.72	0.77	0.69	0.51	0.53	0.74	0.69	0.40	0.56	0.68	0.70	0.62	0.79	0.75	0.59	0.73
321.50		0.83	0.39	0.42	0.79	0.46	0.82	0.40	0.77	0.80	0.72	0.78	0.69	0.57	0.57	0.75	0.59	0.40	0.57	0.74	0.71	0.63	0.80	0.75	0.60	0.74
322.31		0.90	0.49	0.43	0.79	0.46	0.82	0.42	0.77	0.81	0.71	0.79	0.69	0.55	0.54	0.75	0.78	0.40	0.54	0.73	0.72	0.65	0.80	0.82	0.50	0.79
323.11		0.91	0.50	0.44	0.80	0.47	0.83	0.40	0.78	0.82	0.71	0.79	0.77	0.58	0.58	0.75	0.69	0.41	0.54	0.77	0.73	0.65	0.80	0.82	0.61	0.79
323.91		0.91	0.51	0.44	0.80	0.47	0.83	0.44	0.78	0.82	0.72	0.80	0.68	0.51	0.58	0.76	0.73	0.43	0.55	0.79	0.73	0.66	0.80	0.82	0.48	0.79
324.71		0.92	0.53	0.45	0.81	0.47	0.83	0.41	0.78	0.82	0.72	0.80	0.64	0.49	0.53	0.76	0.82	0.41	0.54	0.71	0.74	0.67	0.80	0.82	0.60	0.79
325.51		0.93	0.54	0.45	0.81	0.48	0.84	0.40	0.79	0.84	0.73	0.81	0.72	0.59	0.63	0.76	0.71	0.41	0.55	0.72	0.74	0.68	0.80	0.82	0.46	0.79
326.32		0.93	0.55	0.46	0.81	0.48	0.84	0.43	0.79	0.84	0.73	0.81	0.76	0.58	0.61	0.77	0.77	0.42	0.56	0.69	0.75	0.69	0.81	0.82	0.50	0.78
327.12		0.94	0.56	0.46	0.81	0.48	0.84	0.41	0.80	0.84	0.74	0.81	0.70	0.60	0.57	0.77	0.73	0.42	0.57	0.77	0.75	0.70	0.80	0.82	0.54	0.79
327.92		0.95	0.57	0.46	0.81	0.48	0.85	0.44	0.80	0.84	0.75	0.81	0.66	0.61	0.70	0.78	0.77	0.43	0.58	0.78	0.76	0.70	0.81	0.83	0.46	0.79
328.72		0.96	0.58	0.46	0.81	0.48	0.85	0.44	0.80	0.85	0.76	0.81	0.69	0.55	0.58	0.78	0.79	0.46	0.58	0.73	0.77	0.71	0.81	0.84	0.51	0.80
329.52		0.96	0.59	0.47	0.81	0.49	0.85	0.45	0.80	0.86	0.77	0.81	0.67	0.57	0.67	0.79	0.74	0.46	0.59	0.77	0.77	0.72	0.81	0.84	0.54	0.80
330.33		0.97	0.60	0.48	0.81	0.49	0.86	0.47	0.81	0.86	0.77	0.81	0.76	0.59	0.60	0.79	0.78	0.47	0.59	0.79	0.77	0.72	0.82	0.84	0.58	0.81
331.13		0.97	0.61	0.48	0.81	0.49	0.86	0.47	0.81	0.86	0.78	0.82	0.70	0.54	0.60	0.80	0.72	0.48	0.60	0.81	0.78	0.73	0.82	0.85	0.59	0.82
331.93		0.98	0.62	0.49	0.81	0.49	0.86	0.47	0.81	0.86	0.78	0.82	0.78	0.62	0.65	0.80	0.74	0.49	0.61	0.82	0.78	0.73	0.83	0.85	0.67	0.83
332.73		0.98	0.62	0.49	0.81	0.50	0.86	0.45	0.81	0.87	0.79	0.82	0.68	0.56	0.69	0.81	0.85	0.48	0.61	0.79	0.78	0.74	0.83	0.85	0.63	0.83
333.53		0.98	0.63	0.49	0.81	0.50	0.87	0.49	0.81	0.87	0.80	0.82	0.90	0.61	0.65	0.81	0.83	0.48	0.61	0.84	0.79	0.75	0.83	0.85	0.61	0.83
334.33		0.98	0.63	0.50	0.81	0.50	0.87	0.48	0.81	0.87	0.80	0.82	0.76	0.60	0.60	0.81	0.75	0.49	0.61	0.82	0.79	0.75	0.83	new	0.64	0.83
335.13		0.99	0.64	0.50	0.81	0.50	0.87	0.49	0.81	0.87	0.80	0.82	0.77	0.63	0.59	0.81	0.78	0.49	0.62	0.77	0.79	0.75	0.83	0.85	0.64	0.83

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
335.93		0.99	0.65	0.50	0.81	0.51	0.87	0.50	0.81	0.87	0.80	0.82	0.77	0.69	0.69	0.81	0.77	0.50	0.63	0.80	0.80	0.76	0.82	0.86	0.62	0.83
336.74		0.98	0.65	0.50	0.81	0.51	0.87	0.49	0.81	0.88	0.80	0.82	0.73	0.55	0.69	0.82	0.74	0.52	0.63	0.81	0.80	0.77	0.83	0.85	0.59	0.82
337.54		0.99	0.65	0.51	0.81	0.51	0.87	0.49	0.81	0.89	0.80	0.82	0.77	0.60	0.61	0.82	0.77	0.51	0.63	0.85	0.80	0.77	0.83	0.85	0.54	0.82
338.34		0.98	0.66	0.51	0.81	0.52	0.87	0.49	0.81	0.88	0.80	0.82	0.81	0.71	0.62	0.82	0.74	0.54	0.63	0.81	0.80	0.78	0.83	0.86	0.67	0.83
339.14		0.99	0.67	0.51	0.81	0.52	0.87	0.50	0.81	0.89	0.80	0.82	0.78	0.67	0.67	0.82	0.82	0.53	0.64	0.81	0.81	0.78	0.84	0.86	0.58	0.83
339.94		0.99	0.67	0.52	0.81	0.52	0.87	0.52	0.82	0.89	0.80	0.83	0.78	0.65	0.63	0.82	0.79	0.53	0.64	0.83	0.81	0.79	0.85	0.86	0.57	0.83
340.74		0.98	0.67	0.53	0.81	0.52	0.87	0.51	0.83	0.89	0.80	0.83	0.79	0.65	0.71	0.82	0.83	0.55	0.64	0.77	0.81	0.79	0.85	0.87	0.57	0.84
341.54		0.98	0.67	0.53	0.81	0.52	0.87	0.52	0.83	0.89	0.80	0.83	0.73	0.69	0.69	0.83	0.77	0.54	0.65	0.87	0.82	0.79	0.86	0.87	0.56	0.84
342.34		0.99	0.67	0.54	0.81	0.52	0.88	0.54	0.83	0.88	0.81	0.83	0.71	0.62	0.63	0.83	0.70	0.55	0.65	0.86	0.82	0.79	0.87	0.88	0.67	0.85
343.14		0.98	0.68	0.54	0.81	0.53	0.88	0.56	0.84	0.88	0.81	0.83	0.71	0.63	0.67	0.83	0.78	0.55	0.66	0.85	0.82	0.80	0.87	0.88	0.55	0.85
343.94		0.99	0.69	0.55	0.80	0.53	0.88	0.54	0.84	0.89	0.81	0.84	0.75	0.69	0.69	0.84	0.83	0.57	0.66	0.82	0.82	0.80	0.87	0.88	0.62	0.85
344.74		0.99	0.69	0.55	0.80	0.53	0.88	0.57	0.84	0.89	0.81	0.84	0.77	0.65	0.63	0.84	0.84	0.55	0.66	0.82	0.82	0.80	0.86	0.88	0.63	0.85
345.54		0.99	0.69	0.56	0.80	0.53	0.88	0.60	0.85	0.89	0.81	0.84	0.82	0.68	0.73	0.84	0.77	0.57	0.66	0.78	0.83	0.81	0.86	0.88	0.61	0.85
346.34		0.99	0.70	0.56	0.80	0.53	0.88	0.57	0.84	0.90	0.82	0.84	0.78	0.71	0.67	0.84	0.87	0.58	0.67	0.83	0.83	0.81	0.86	0.88	0.63	0.85
347.14		0.99	0.70	0.56	0.80	0.53	0.89	0.60	0.84	0.90	0.83	0.84	0.78	0.65	0.68	0.84	0.89	0.57	0.68	0.80	0.83	0.81	0.86	0.88	0.58	0.85
347.94		1.00	0.71	0.56	0.80	0.54	0.89	0.59	0.84	0.91	0.83	0.84	0.76	0.69	0.74	0.84	0.80	0.59	0.68	0.87	0.84	0.82	0.86	0.88	0.65	0.85
348.74		0.99	0.70	0.56	0.80	0.54	0.89	0.61	0.84	0.91	0.83	0.84	0.79	0.66	0.64	0.84	0.74	0.59	0.68	0.83	0.84	0.82	0.86	0.89	0.59	0.86
349.54		0.99	0.70	0.57	0.80	0.54	0.89	0.60	0.84	0.91	0.83	0.84	0.84	0.67	0.71	0.84	0.82	0.60	0.68	0.83	0.84	0.82	0.87	0.88	0.62	0.86
350.34		0.99	0.70	0.57	0.80	0.54	0.90	0.58	0.84	0.91	0.83	0.84	0.87	0.72	0.74	0.85	0.84	0.60	0.69	0.87	0.85	0.83	0.86	0.88	0.56	0.86
351.14		0.99	0.71	0.58	0.80	0.55	0.90	0.62	0.84	0.91	0.83	0.84	0.81	0.67	0.72	0.86	0.78	0.60	0.69	0.84	0.84	0.83	0.87	0.88	0.53	0.86
351.94		0.99	0.71	0.58	0.79	0.55	0.90	0.61	0.84	0.91	0.83	0.85	0.83	0.68	0.69	0.85	0.82	0.62	0.69	0.80	0.84	0.83	0.87	0.88	0.56	0.86
352.74		0.99	0.71	0.59	0.79	0.55	0.90	0.61	0.85	0.91	0.83	0.85	0.73	0.72	0.69	0.86	0.84	0.63	0.69	0.84	0.84	0.84	0.86	0.88	0.69	0.86
353.54		0.99	0.71	0.60	0.79	0.55	0.90	0.64	0.85	0.91	0.83	0.85	0.76	0.66	0.79	0.86	0.83	0.63	0.69	0.79	0.85	0.84	0.87	0.88	0.67	0.86
354.34		1.00	0.72	0.60	0.79	0.55	0.90	0.62	0.85	0.91	0.84	0.85	0.85	0.74	0.70	0.87	0.75	0.61	0.70	0.82	0.85	0.84	0.87	0.88	0.64	0.86

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
355.14		1.00	0.73	0.60	0.79	0.56	0.90	0.64	0.86	0.91	0.84	0.85	0.78	0.69	0.75	0.87	0.81	0.62	0.71	0.86	0.85	0.84	0.87	0.89	0.61	0.86
355.94		1.00	0.73	0.60	0.79	0.56	0.90	0.66	0.86	0.91	0.84	0.85	0.80	0.75	0.71	0.87	0.85	0.63	0.70	0.80	0.85	0.84	0.87	0.89	0.54	0.87
356.74		0.99	0.73	0.60	0.79	0.56	0.91	0.65	0.86	0.92	0.84	0.86	0.77	0.72	0.74	0.86	0.86	0.64	0.70	0.86	0.85	0.85	0.87	0.89	0.62	0.87
357.54		0.99	0.73	0.61	0.79	0.56	0.91	0.66	0.86	0.92	0.84	0.86	0.80	0.69	0.69	0.86	0.82	0.64	0.70	0.84	0.85	0.85	0.88	0.90	0.62	0.87
358.34		0.99	0.73	0.61	0.79	0.57	0.90	0.64	0.86	0.92	0.84	0.86	0.69	0.72	0.70	0.86	0.85	0.66	0.71	0.90	0.85	0.85	0.88	0.90	0.62	0.87
359.14		0.99	0.73	0.61	0.79	0.57	0.90	0.66	0.87	0.92	0.84	0.86	0.87	0.70	0.72	0.86	0.89	0.66	0.71	0.84	0.85	0.85	0.88	0.90	0.63	0.87
359.94		0.99	0.73	0.62	0.79	0.57	0.91	0.66	0.87	0.93	0.85	0.86	0.75	0.73	0.67	0.86	0.79	0.66	0.72	0.84	0.85	0.85	0.88	0.89	0.60	0.87
360.74		0.99	0.74	0.62	0.79	0.57	0.91	0.67	0.87	0.93	0.84	0.87	0.80	0.71	0.73	0.87	0.80	0.67	0.71	0.82	0.85	0.85	0.88	0.89	0.60	0.87
361.53		0.99	0.74	0.63	0.79	0.57	0.91	0.65	0.88	0.93	0.84	0.88	0.81	0.76	0.75	0.87	0.74	0.67	0.71	0.84	0.86	0.86	0.88	0.90	0.55	0.87
362.33		0.99	0.74	0.63	0.78	0.58	0.91	0.70	0.88	0.93	0.84	0.87	0.75	0.77	0.70	0.87	0.79	0.68	0.72	0.90	0.86	0.86	0.88	0.90	0.61	0.88
363.13		0.99	0.74	0.63	0.78	0.58	0.91	0.68	0.87	0.93	0.84	0.87	0.74	0.73	0.70	0.87	0.99	0.66	0.72	0.89	0.86	0.86	0.88	0.90	0.61	0.88
363.93		0.99	0.74	0.63	0.78	0.58	0.91	0.68	0.88	0.93	0.84	0.87	0.79	0.73	0.70	0.87	0.78	0.68	0.72	0.86	0.86	0.86	0.88	0.90	0.62	0.88
364.73		0.99	0.75	0.64	0.78	0.58	0.91	0.71	0.87	0.93	0.84	0.87	0.79	0.74	0.71	0.88	0.86	0.68	0.72	0.83	0.86	0.86	0.88	0.91	0.64	0.89
365.53		0.99	0.75	0.63	0.78	0.58	0.91	0.71	0.87	0.93	0.84	0.87	0.81	0.68	0.71	0.88	0.80	0.68	0.72	0.87	0.86	0.86	0.88	0.91	0.60	0.89
366.33		0.99	0.75	0.64	0.78	0.59	0.91	0.70	0.86	0.93	0.85	0.87	0.79	0.74	0.71	0.88	0.83	0.69	0.72	0.88	0.86	0.87	0.89	0.90	0.60	0.89
367.12		0.99	0.75	0.64	0.78	0.59	0.91	0.68	0.86	0.93	0.85	0.87	0.83	0.72	0.69	0.88	0.81	0.70	0.73	0.80	0.87	0.87	0.89	0.91	0.60	0.89
367.92		0.99	0.76	0.64	0.79	0.59	0.91	0.70	0.86	0.93	0.85	0.87	0.84	0.75	0.78	0.89	0.87	0.70	0.73	0.82	0.87	0.87	0.88	0.91	0.58	0.89
368.72		0.99	0.76	0.65	0.79	0.59	0.91	0.73	0.87	0.93	0.85	0.87	0.76	0.81	0.73	0.89	0.79	0.70	0.73	0.86	0.87	0.87	0.88	0.91	0.60	0.89
369.52		0.99	0.76	0.65	0.79	0.59	0.91	0.72	0.86	0.94	0.85	0.87	0.76	0.75	0.78	0.90	0.89	0.68	0.73	0.87	0.87	0.87	0.88	0.91	0.66	0.89
370.32		0.99	0.76	0.66	0.79	0.59	0.91	0.73	0.86	0.94	0.86	0.87	0.82	0.72	0.69	0.89	0.80	0.70	0.74	0.85	0.87	0.87	0.89	0.91	0.61	0.88
371.12		1.00	0.76	0.66	0.79	0.60	0.91	0.73	0.86	0.94	0.86	0.87	0.70	0.72	0.76	0.89	0.87	0.70	0.74	0.86	0.87	0.87	0.88	0.90	0.67	0.88
371.91		1.00	0.77	0.66	0.79	0.60	0.92	0.73	0.87	0.94	0.85	0.87	0.80	0.74	0.74	0.89	0.89	0.71	0.74	0.82	0.87	0.87	0.88	0.91	0.63	0.89
372.71		1.00	0.77	0.66	0.79	0.60	0.92	0.72	0.87	0.94	0.85	0.87	0.86	0.69	0.68	0.89	0.84	0.71	0.75	0.85	0.87	0.87	0.89	0.90	0.56	0.89
373.51		1.00	0.78	0.66	0.79	0.60	0.92	0.74	0.87	0.95	0.85	0.87	0.84	0.76	0.75	0.88	0.85	0.71	0.75	0.85	0.88	0.88	0.89	0.91	0.59	0.89

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
374.31		1.00	0.77	0.66	0.80	0.60	0.92	0.73	0.87	0.95	0.85	0.88	0.84	0.80	0.69	0.88	0.81	0.72	0.75	0.89	0.88	0.88	0.89	0.91	0.56	0.89
375.10		1.00	0.77	0.66	0.80	0.60	0.92	0.74	0.87	0.95	0.85	0.87	0.82	0.70	0.72	0.88	0.82	0.72	0.75	0.94	0.88	0.88	0.89	0.91	0.65	0.90
375.90		1.00	0.77	0.66	0.80	0.60	0.92	0.75	0.87	0.95	0.85	0.88	0.82	0.71	0.73	0.88	0.80	0.71	0.75	0.85	0.88	0.88	0.89	0.90	0.62	0.90
376.70		1.00	0.77	0.66	0.80	0.59	0.93	0.76	0.88	0.95	0.85	0.88	0.78	0.77	0.69	0.88	0.79	0.73	0.75	0.84	0.88	0.88	0.89	0.90	0.61	0.89
377.50		1.01	0.77	0.66	0.80	0.59	0.93	0.74	0.87	0.95	0.85	0.88	0.82	0.75	0.69	0.88	0.83	0.74	0.75	0.85	0.88	0.88	0.89	0.91	0.62	0.89
378.29		1.00	0.77	0.66	0.80	0.59	0.93	0.74	0.87	0.95	0.85	0.89	0.81	0.73	0.73	0.89	0.85	0.71	0.75	0.89	0.88	0.89	0.89	0.91	0.60	0.89
379.09		1.00	0.77	0.67	0.81	0.59	0.93	0.74	0.87	0.94	0.86	0.89	0.81	0.72	0.70	0.89	0.79	0.72	0.75	0.84	0.88	0.89	0.89	0.91	0.59	0.89
379.89		1.00	0.77	0.67	0.81	0.59	0.93	0.76	0.88	0.94	0.85	0.88	0.75	0.69	0.70	0.88	0.79	0.73	0.75	0.92	0.88	0.89	0.89	0.91	0.62	0.89
380.69		1.01	0.76	0.67	0.81	0.59	0.93	0.75	0.88	0.95	0.85	0.89	0.80	0.68	0.71	0.89	0.79	0.73	0.75	0.85	0.88	0.89	0.89	0.91	0.60	0.89
381.48		1.01	0.76	0.67	0.81	0.59	0.93	0.76	0.88	0.94	0.85	0.90	0.78	0.70	0.76	0.88	0.84	0.73	0.76	0.85	0.89	0.89	0.89	0.92	0.58	0.89
382.28		1.01	0.76	0.67	0.82	0.59	0.93	0.77	0.88	0.94	0.86	0.90	0.74	0.73	0.76	0.88	0.85	0.73	0.75	0.87	0.89	0.89	0.89	0.92	0.62	0.89
383.08		1.01	0.76	0.67	0.82	0.58	0.93	0.77	0.88	0.94	0.86	0.90	0.77	0.71	0.74	0.88	0.82	0.76	0.75	0.88	0.89	0.89	0.89	0.92	0.55	0.89
383.87		1.02	0.75	0.67	0.82	0.58	0.93	0.76	0.88	0.94	0.86	0.90	0.78	0.74	0.71	0.88	0.83	0.75	0.75	0.89	0.89	0.89	0.89	0.92	0.61	0.89
384.67		1.01	0.75	0.67	0.82	0.58	0.93	0.77	0.88	0.94	0.85	0.90	0.78	0.73	0.71	0.88	0.84	0.75	0.75	0.90	0.89	0.89	0.89	0.92	0.61	0.89
385.47		1.01	0.74	0.67	0.83	0.58	0.93	0.79	0.87	0.94	0.85	0.90	0.78	0.71	0.71	0.88	0.95	0.75	0.75	0.92	0.89	0.90	0.90	0.92	0.60	0.89
386.26		1.01	0.74	0.67	0.83	0.57	0.93	0.78	0.87	0.94	0.85	0.90	0.77	0.70	0.71	0.88	0.89	0.76	0.75	0.90	0.89	0.90	0.90	0.92	0.64	0.89
387.06		1.01	0.74	0.67	0.83	0.57	0.93	0.79	0.87	0.94	0.85	0.90	0.79	0.72	0.73	0.88	0.82	0.75	0.76	0.84	0.89	0.90	0.90	0.92	0.59	0.89
387.86		1.01	0.74	0.67	0.84	0.56	0.93	0.79	0.87	0.95	0.84	0.90	0.77	0.69	0.69	0.89	0.78	0.75	0.76	0.85	0.89	0.90	0.90	0.92	0.61	0.89
388.65		1.01	0.74	0.67	0.84	0.56	0.93	0.77	0.86	0.95	0.84	0.90	0.79	0.69	0.73	0.89	0.84	0.75	0.76	0.90	0.89	0.90	0.91	0.92	0.60	0.89
389.45		1.01	0.74	0.68	0.84	0.55	0.93	0.79	0.87	0.94	0.84	0.90	0.77	0.72	0.72	0.89	0.79	0.75	0.76	0.86	0.89	0.90	0.91	0.92	0.58	0.89
390.25		1.01	0.74	0.68	0.85	0.55	0.93	0.77	0.86	0.94	0.84	0.90	0.80	0.72	0.69	0.89	0.83	0.76	0.77	0.89	0.89	0.90	0.91	0.92	0.63	0.89
391.04		1.01	0.74	0.67	0.85	0.54	0.94	0.77	0.87	0.94	0.84	0.90	0.84	0.74	0.70	0.89	0.81	0.75	0.77	0.87	0.90	0.90	0.91	0.92	0.56	0.89
391.84		1.00	0.73	0.68	0.85	0.54	0.94	0.77	0.87	0.94	0.84	0.90	0.86	0.71	0.71	0.89	0.85	0.75	0.77	0.87	0.90	0.90	0.91	0.92	0.56	0.89
392.64		1.00	0.73	0.68	0.86	0.53	0.93	0.76	0.88	0.94	0.84	0.91	0.77	0.69	0.68	0.89	0.84	0.74	0.77	0.88	0.90	0.91	0.91	0.92	0.60	0.89

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
393.43		1.00	0.72	0.67	0.86	0.52	0.94	0.76	0.88	0.94	0.83	0.91	0.79	0.69	0.71	0.88	0.84	0.77	0.77	0.87	0.90	0.91	0.91	0.92	0.58	0.89
394.23		1.00	0.71	0.67	0.86	0.52	0.94	0.77	0.88	0.94	0.83	0.91	0.79	0.69	0.68	0.88	0.83	0.77	0.77	0.87	0.90	0.91	0.91	0.92	0.58	0.89
395.02		1.00	0.70	0.67	0.86	0.51	0.94	0.78	0.88	0.94	0.83	0.92	0.78	0.69	0.67	0.88	0.83	0.76	0.77	0.88	0.90	0.91	0.91	0.92	0.58	0.89
395.82		1.00	0.69	0.67	0.87	0.50	0.94	0.78	0.88	0.94	0.83	0.92	0.81	0.70	0.70	0.88	0.83	0.76	0.77	0.87	0.90	0.91	0.90	0.92	0.56	0.89
396.61		1.00	0.72	0.67	0.87	0.49	0.94	0.80	0.88	0.94	0.87	0.88	0.78	0.68	0.69	0.86	0.83	0.76	0.73	0.86	0.90	0.91	0.90	0.92	0.54	0.89
397.41		1.00	0.72	0.66	0.87	0.49	0.94	0.79	0.87	0.94	0.87	0.88	0.82	0.64	0.67	0.86	0.84	0.77	0.73	0.87	0.90	0.91	0.90	0.92	0.54	0.89
398.21		1.00	0.71	0.66	0.87	0.48	0.94	0.79	0.87	0.94	0.87	0.88	0.79	0.67	0.67	0.85	0.82	0.78	0.73	0.88	0.90	0.91	0.91	0.92	0.54	0.89
399.00		1.00	0.70	0.66	0.88	0.47	0.94	0.77	0.87	0.94	0.87	0.89	0.80	0.67	0.65	0.85	1.01	0.78	0.73	0.82	0.90	0.91	0.91	0.92	0.36	0.89
399.80		1.00	0.70	0.66	0.88	0.46	0.94	0.78	0.87	0.94	0.87	0.89	0.78	0.70	0.69	0.85	0.85	0.76	0.73	0.86	0.90	0.91	0.91	0.92	0.53	0.89
400.59		1.00	0.69	0.66	0.88	0.46	0.94	0.79	0.87	0.94	0.87	0.89	0.82	0.62	0.65	0.84	0.86	0.77	0.73	0.90	0.90	0.91	0.90	0.91	0.52	0.89
401.39		1.00	0.68	0.66	0.89	0.45	0.94	0.79	0.87	0.94	0.87	0.89	0.83	0.66	0.70	0.84	0.85	0.77	0.74	0.89	0.90	0.91	0.91	0.92	0.53	0.89
402.18		1.01	0.64	0.66	0.89	0.44	0.94	0.77	0.87	0.94	0.83	0.93	0.82	0.67	0.67	0.86	0.84	0.78	0.78	0.89	0.90	0.91	0.91	0.91	0.54	0.88
402.98		1.00	0.63	0.66	0.89	0.43	0.94	0.77	0.87	0.94	0.83	0.93	0.81	0.69	0.66	0.86	0.84	0.78	0.78	0.86	0.90	0.91	0.91	0.92	0.51	0.89
403.77		1.01	0.63	0.66	0.90	0.42	0.94	0.79	0.86	0.94	0.83	0.93	0.80	0.66	0.64	0.85	0.86	0.78	0.77	0.88	0.90	0.91	0.91	0.91	0.53	0.89
404.57		1.01	0.63	0.66	0.90	0.41	0.94	0.79	0.86	0.94	0.83	0.92	0.81	0.63	0.65	0.85	0.84	0.77	0.77	0.85	0.90	0.91	0.91	0.92	0.50	0.89
405.36		1.01	0.62	0.65	0.90	0.40	0.94	0.80	0.85	0.94	0.83	0.92	0.79	0.65	0.64	0.85	0.84	0.77	0.78	0.87	0.90	0.91	0.91	0.92	0.51	0.89
406.16		1.01	0.62	0.65	0.90	0.39	0.94	0.78	0.85	0.94	0.83	0.92	0.81	0.61	0.62	0.85	0.86	0.77	0.78	0.89	0.90	0.91	0.91	0.92	0.49	0.89
406.95		1.01	0.62	0.65	0.91	0.39	0.94	0.80	0.84	0.94	0.83	0.92	0.79	0.61	0.65	0.84	0.84	0.77	0.78	0.87	0.91	0.91	0.91	0.92	0.49	0.89
407.75		1.01	0.61	0.65	0.91	0.38	0.94	0.79	0.84	0.94	0.83	0.92	0.79	0.62	0.62	0.84	0.87	0.77	0.78	0.89	0.91	0.91	0.91	0.92	0.47	0.89
408.54		1.01	0.61	0.65	0.91	0.37	0.94	0.79	0.84	0.94	0.83	0.92	0.83	0.63	0.65	0.83	0.85	0.78	0.79	0.87	0.91	0.92	0.91	0.92	0.48	0.89
409.34		1.01	0.61	0.65	0.91	0.36	0.94	0.81	0.84	0.94	0.83	0.92	0.82	0.62	0.64	0.83	0.85	0.79	0.79	0.87	0.91	0.92	0.92	0.92	0.51	0.89
410.13		1.00	0.60	0.65	0.91	0.36	0.94	0.79	0.84	0.94	0.83	0.93	0.82	0.63	0.63	0.83	0.86	0.77	0.79	0.89	0.91	0.92	0.92	0.92	0.47	0.89
410.93		1.00	0.60	0.66	0.92	0.35	0.94	0.79	0.84	0.94	0.83	0.93	0.83	0.63	0.63	0.83	0.85	0.78	0.79	0.90	0.91	0.92	0.92	0.92	0.47	0.88
411.72		1.00	0.60	0.66	0.92	0.35	0.94	0.79	0.85	0.94	0.82	0.93	0.81	0.62	0.63	0.83	0.85	0.77	0.80	0.91	0.91	0.92	0.92	0.92	0.48	0.88

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
412.51		1.00	0.60	0.66	0.92	0.35	0.94	0.80	0.85	0.94	0.83	0.93	0.80	0.62	0.64	0.83	0.85	0.78	0.80	0.87	0.91	0.92	0.92	0.92	0.47	0.89
413.31		1.00	0.60	0.66	0.92	0.35	0.94	0.80	0.85	0.94	0.83	0.94	0.80	0.62	0.63	0.83	0.87	0.78	0.80	0.89	0.91	0.92	0.92	0.92	0.47	0.88
414.10		1.00	0.61	0.67	0.92	0.35	0.94	0.80	0.85	0.94	0.83	0.94	0.80	0.64	0.63	0.83	0.88	0.78	0.80	0.88	0.91	0.92	0.92	0.92	0.47	0.89
414.90		1.00	0.61	0.67	0.92	0.35	0.94	0.79	0.85	0.94	0.84	0.94	0.80	0.62	0.62	0.83	0.89	0.79	0.80	0.88	0.91	0.92	0.92	0.92	0.48	0.89
415.69		1.00	0.61	0.67	0.93	0.35	0.94	0.79	0.85	0.94	0.83	0.94	0.81	0.61	0.61	0.83	0.85	0.78	0.81	0.90	0.91	0.92	0.92	0.92	0.50	0.89
416.48		0.99	0.62	0.68	0.93	0.35	0.94	0.80	0.85	0.94	0.84	0.94	0.87	0.61	0.66	0.83	0.87	0.78	0.81	0.87	0.91	0.92	0.93	0.92	0.50	0.89
417.28		1.00	0.62	0.68	0.93	0.36	0.94	0.81	0.85	0.94	0.84	0.94	0.80	0.62	0.64	0.83	0.85	0.79	0.81	0.86	0.91	0.92	0.93	0.91	0.48	0.89
418.07		1.00	0.62	0.68	0.93	0.36	0.94	0.80	0.85	0.94	0.84	0.94	0.81	0.65	0.64	0.83	0.87	0.79	0.81	0.88	0.91	0.93	0.93	0.91	0.52	0.89
418.87		1.00	0.63	0.69	0.94	0.37	0.94	0.80	0.85	0.94	0.84	0.94	0.84	0.61	0.66	0.84	0.84	0.79	0.81	0.88	0.91	0.93	0.94	0.91	0.52	0.89
419.66		1.00	0.64	0.69	0.94	0.37	0.94	0.80	0.85	0.94	0.84	0.94	0.82	0.64	0.65	0.84	0.87	0.80	0.81	0.89	0.92	0.93	0.94	0.92	0.51	0.89
420.45		1.00	0.65	0.70	0.94	0.38	0.94	0.79	0.86	0.94	0.84	0.94	0.84	0.64	0.64	0.84	0.85	0.79	0.82	0.92	0.92	0.93	0.94	0.91	0.52	0.90
421.25		1.01	0.66	0.70	0.94	0.39	0.94	0.80	0.86	0.94	0.84	0.94	0.83	0.64	0.68	0.85	0.87	0.80	0.82	0.89	0.91	0.93	0.95	0.92	0.55	0.90
422.04		1.01	0.67	0.71	0.94	0.40	0.94	0.80	0.86	0.94	0.84	0.94	0.80	0.67	0.67	0.85	0.88	0.80	0.82	0.90	0.92	0.93	0.95	0.92	0.56	0.90
422.83		1.01	0.68	0.71	0.95	0.41	0.95	0.82	0.86	0.95	0.84	0.94	0.82	0.67	0.68	0.86	0.84	0.80	0.82	0.90	0.92	0.93	0.94	0.92	0.57	0.90
423.63		1.01	0.69	0.71	0.95	0.43	0.95	0.81	0.86	0.95	0.84	0.94	0.86	0.67	0.68	0.86	0.87	0.79	0.82	0.89	0.92	0.93	0.95	0.92	0.59	0.90
424.42		1.01	0.70	0.72	0.95	0.44	0.95	0.82	0.87	0.95	0.85	0.94	0.84	0.67	0.68	0.86	0.85	0.81	0.83	0.88	0.92	0.93	0.95	0.93	0.61	0.90
425.21		1.01	0.71	0.72	0.95	0.45	0.95	0.82	0.87	0.95	0.85	0.94	0.83	0.67	0.70	0.87	0.86	0.81	0.83	0.91	0.92	0.93	0.95	0.93	0.60	0.91
426.01		1.02	0.72	0.73	0.95	0.47	0.95	0.81	0.87	0.95	0.85	0.94	0.85	0.67	0.72	0.87	0.86	0.80	0.83	0.89	0.92	0.93	0.95	0.93	0.63	0.90
426.80		1.01	0.74	0.74	0.96	0.49	0.95	0.82	0.88	0.95	0.85	0.95	0.85	0.69	0.72	0.88	0.88	0.81	0.83	0.91	0.92	0.94	0.94	0.93	0.62	0.91
427.59		1.01	0.74	0.74	0.96	0.50	0.95	0.82	0.87	0.95	0.85	0.95	0.85	0.73	0.75	0.88	0.86	0.81	0.84	0.89	0.92	0.94	0.95	0.93	0.66	0.91
428.38		1.01	0.75	0.74	0.96	0.52	0.95	0.83	0.88	0.95	0.86	0.95	0.86	0.72	0.75	0.88	0.86	0.81	0.84	0.90	0.92	0.94	0.95	0.93	0.64	0.91
429.18		1.01	0.76	0.75	0.96	0.53	0.95	0.83	0.88	0.95	0.86	0.95	0.86	0.70	0.74	0.89	0.86	0.80	0.84	0.88	0.92	0.94	0.94	0.94	0.65	0.91
429.97		1.01	0.78	0.75	0.96	0.55	0.95	0.84	0.87	0.95	0.86	0.95	0.85	0.74	0.75	0.89	0.86	0.81	0.84	0.90	0.93	0.94	0.94	0.94	0.67	0.91
430.76		1.01	0.78	0.76	0.96	0.56	0.95	0.82	0.87	0.95	0.86	0.95	0.85	0.73	0.76	0.89	0.89	0.81	0.85	0.90	0.93	0.94	0.94	0.94	0.68	0.91

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
431.56		1.01	0.79	0.76	0.96	0.57	0.95	0.83	0.87	0.95	0.86	0.95	0.87	0.76	0.76	0.90	0.87	0.81	0.85	0.91	0.93	0.94	0.94	0.94	0.69	0.92
432.35		1.02	0.80	0.76	0.96	0.59	0.95	0.84	0.88	0.95	0.87	0.95	0.86	0.75	0.75	0.90	0.88	0.82	0.86	0.91	0.93	0.94	0.94	0.94	0.73	0.91
433.14		1.02	0.81	0.77	0.96	0.60	0.96	0.83	0.88	0.96	0.87	0.95	0.88	0.78	0.78	0.91	0.87	0.82	0.86	0.89	0.93	0.94	0.94	0.94	0.69	0.92
433.93		1.02	0.82	0.77	0.97	0.62	0.96	0.84	0.89	0.96	0.87	0.95	0.85	0.76	0.78	0.92	0.88	0.82	0.86	0.91	0.93	0.94	0.94	0.95	0.69	0.92
434.73		1.02	0.82	0.77	0.97	0.63	0.96	0.83	0.89	0.95	0.88	0.95	0.90	0.76	0.79	0.92	0.89	0.83	0.86	0.90	0.93	0.94	0.94	0.95	0.73	0.92
435.52		1.02	0.82	0.78	0.97	0.64	0.96	0.84	0.89	0.96	0.88	0.96	0.88	0.76	0.78	0.92	0.87	0.82	0.86	0.92	0.94	0.94	0.94	0.95	0.74	0.92
436.31		1.02	0.83	0.78	0.97	0.66	0.96	0.83	0.90	0.96	0.88	0.96	0.88	0.78	0.79	0.92	0.89	0.82	0.86	0.91	0.94	0.95	0.94	0.95	0.75	0.92
437.10		1.02	0.84	0.78	0.97	0.67	0.96	0.84	0.90	0.96	0.88	0.95	0.89	0.79	0.79	0.92	0.90	0.82	0.86	0.91	0.94	0.94	0.94	0.95	0.75	0.92
437.89		1.02	0.85	0.79	0.97	0.68	0.96	0.84	0.90	0.96	0.88	0.95	0.88	0.77	0.81	0.92	0.89	0.82	0.86	0.91	0.94	0.95	0.94	0.95	0.76	0.92
438.69		1.02	0.85	0.79	0.97	0.69	0.96	0.84	0.90	0.96	0.88	0.95	0.90	0.78	0.80	0.92	0.87	0.83	0.86	0.91	0.94	0.94	0.94	0.95	0.76	0.92
439.48		1.02	0.85	0.79	0.97	0.70	0.96	0.84	0.90	0.96	0.88	0.95	0.90	0.77	0.80	0.92	0.89	0.83	0.86	0.92	0.94	0.94	0.94	0.95	0.77	0.92
440.27		1.02	0.86	0.79	0.98	0.71	0.96	0.85	0.90	0.96	0.88	0.95	0.90	0.81	0.80	0.93	0.88	0.83	0.86	0.91	0.94	0.94	0.94	0.95	0.78	0.93
441.06		1.01	0.87	0.80	0.98	0.72	0.96	0.84	0.90	0.96	0.88	0.95	0.87	0.79	0.82	0.93	0.87	0.84	0.86	0.89	0.94	0.95	0.94	0.95	0.77	0.92
441.85		1.01	0.87	0.80	0.98	0.73	0.96	0.85	0.90	0.96	0.88	0.95	0.88	0.79	0.82	0.93	0.87	0.82	0.87	0.91	0.94	0.95	0.94	0.95	0.78	0.93
442.64		1.01	0.87	0.80	0.98	0.74	0.96	0.84	0.91	0.96	0.88	0.95	0.89	0.79	0.83	0.93	0.89	0.83	0.87	0.92	0.94	0.95	0.94	0.95	0.79	0.93
443.44		1.01	0.87	0.81	0.98	0.74	0.96	0.85	0.91	0.96	0.88	0.95	0.90	0.80	0.82	0.94	0.89	0.83	0.87	0.93	0.94	0.95	0.94	0.95	0.77	0.93
444.23		1.01	0.88	0.81	0.98	0.75	0.96	0.85	0.91	0.96	0.88	0.95	0.89	0.81	0.83	0.94	0.87	0.84	0.87	0.93	0.94	0.95	0.94	0.95	0.79	0.93
445.02		1.01	0.88	0.81	0.98	0.76	0.96	0.86	0.91	0.96	0.88	0.96	0.88	0.79	0.83	0.94	0.89	0.83	0.87	0.91	0.94	0.95	0.94	0.95	0.80	0.93
445.81		1.01	0.88	0.82	0.98	0.76	0.96	0.86	0.91	0.96	0.89	0.96	0.90	0.80	0.83	0.94	0.89	0.83	0.88	0.91	0.94	0.95	0.95	0.96	0.82	0.93
446.60		1.02	0.88	0.82	0.98	0.77	0.96	0.86	0.91	0.95	0.89	0.96	0.88	0.79	0.83	0.94	0.87	0.84	0.88	0.91	0.94	0.95	0.95	0.95	0.83	0.93
447.39		1.02	0.89	0.82	0.98	0.77	0.96	0.86	0.91	0.96	0.89	0.96	0.90	0.81	0.85	0.94	0.87	0.83	0.88	0.92	0.94	0.95	0.95	0.95	0.82	0.92
448.18		1.02	0.89	0.82	0.98	0.78	0.96	0.85	0.91	0.96	0.90	0.96	0.89	0.81	0.83	0.94	0.90	0.84	0.88	0.90	0.94	0.95	0.95	0.96	0.82	0.93
448.97		1.02	0.89	0.82	0.98	0.78	0.96	0.85	0.91	0.96	0.90	0.96	0.89	0.80	0.84	0.94	0.89	0.84	0.87	0.90	0.94	0.95	0.95	0.95	0.82	0.92
449.76		1.02	0.89	0.82	0.98	0.79	0.96	0.86	0.91	0.96	0.89	0.96	0.89	0.83	0.84	0.94	0.89	0.84	0.88	0.93	0.94	0.95	0.95	0.95	0.82	0.92

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
450.56		1.02	0.89	0.82	0.98	0.79	0.97	0.86	0.91	0.96	0.90	0.96	0.90	0.82	0.84	0.95	0.90	0.84	0.88	0.91	0.94	0.95	0.95	0.95	0.85	0.93
451.35		1.02	0.90	0.82	0.98	0.79	0.96	0.86	0.91	0.96	0.89	0.96	0.89	0.82	0.85	0.95	0.87	0.84	0.88	0.91	0.94	0.95	0.95	0.95	0.84	0.93
452.14		1.02	0.90	0.83	0.98	0.80	0.97	0.87	0.91	0.97	0.90	0.96	0.91	0.81	0.86	0.95	0.89	0.84	0.88	0.92	0.95	0.95	0.95	0.96	0.83	0.93
452.93		1.02	0.90	0.83	0.98	0.80	0.97	0.86	0.91	0.97	0.89	0.96	0.91	0.82	0.86	0.95	0.88	0.84	0.88	0.91	0.95	0.95	0.95	0.96	0.84	0.93
453.72		1.02	0.90	0.83	0.99	0.81	0.97	0.86	0.91	0.97	0.90	0.96	0.92	0.80	0.85	0.95	0.90	0.84	0.88	0.92	0.95	0.95	0.95	0.96	0.84	0.93
454.51		1.02	0.90	0.83	0.99	0.81	0.97	0.86	0.92	0.97	0.90	0.96	0.90	0.81	0.85	0.95	0.90	0.84	0.88	0.91	0.95	0.95	0.95	0.96	0.82	0.93
455.30		1.02	0.90	0.83	0.99	0.81	0.97	0.86	0.92	0.97	0.90	0.96	0.90	0.82	0.85	0.95	0.87	0.85	0.88	0.93	0.95	0.95	0.95	0.96	0.85	0.94
456.09		1.02	0.91	0.83	0.99	0.81	0.97	0.86	0.92	0.96	0.90	0.96	0.91	0.83	0.87	0.95	0.89	0.84	0.88	0.92	0.95	0.95	0.95	0.96	0.84	0.93
456.88		1.02	0.91	0.83	0.99	0.82	0.97	0.86	0.92	0.97	0.90	0.96	0.91	0.82	0.87	0.96	0.90	0.85	0.88	0.92	0.95	0.95	0.95	0.96	0.83	0.93
457.67		1.02	0.91	0.83	0.99	0.82	0.97	0.86	0.92	0.96	0.90	0.96	0.91	0.84	0.85	0.96	0.88	0.85	0.88	0.94	0.95	0.95	0.95	0.96	0.84	0.94
458.46		1.02	0.91	0.84	0.99	0.82	0.97	0.87	0.92	0.97	0.89	0.96	0.91	0.82	0.88	0.95	0.90	0.84	0.88	0.91	0.95	0.96	0.95	0.96	0.86	0.94
459.25		1.02	0.91	0.84	0.99	0.83	0.97	0.87	0.92	0.97	0.90	0.96	0.91	0.82	0.87	0.95	0.89	0.85	0.89	0.92	0.95	0.96	0.95	0.96	0.86	0.94
460.04		1.03	0.91	0.84	0.99	0.83	0.97	0.86	0.92	0.97	0.90	0.96	0.90	0.84	0.86	0.95	0.91	0.85	0.89	0.93	0.95	0.96	0.95	0.96	0.85	0.94
460.83		1.03	0.91	0.84	0.99	0.83	0.97	0.86	0.92	0.97	0.90	0.96	0.92	0.84	0.86	0.96	0.89	0.84	0.89	0.93	0.95	0.96	0.95	0.96	0.86	0.94
461.62		1.03	0.91	0.84	0.99	0.83	0.97	0.87	0.92	0.97	0.90	0.96	0.92	0.84	0.86	0.96	0.89	0.85	0.89	0.91	0.95	0.96	0.95	0.96	0.85	0.94
462.41		1.03	0.92	0.85	0.99	0.83	0.97	0.87	0.92	0.97	0.90	0.97	0.92	0.84	0.87	0.96	0.88	0.85	0.89	0.94	0.95	0.96	0.95	0.96	0.84	0.94
463.20		1.02	0.92	0.85	0.99	0.84	0.97	0.87	0.92	0.97	0.90	0.97	0.93	0.83	0.87	0.95	0.90	0.85	0.89	0.93	0.95	0.96	0.95	0.96	0.87	0.94
463.99		1.02	0.92	0.85	0.99	0.84	0.97	0.88	0.92	0.97	0.90	0.97	0.92	0.82	0.88	0.96	0.89	0.85	0.89	0.92	0.95	0.96	0.95	0.96	0.85	0.94
464.78		1.02	0.92	0.85	0.99	0.84	0.97	0.87	0.92	0.97	0.90	0.96	0.91	0.84	0.88	0.96	0.90	0.85	0.89	0.91	0.95	0.96	0.95	0.96	0.86	0.94
465.57		1.02	0.92	0.85	0.99	0.84	0.97	0.87	0.92	0.97	0.90	0.96	0.92	0.82	0.87	0.96	0.90	0.85	0.89	0.93	0.95	0.96	0.95	0.96	0.87	0.94
466.36		1.02	0.92	0.85	0.99	0.84	0.97	0.88	0.92	0.96	0.90	0.96	0.92	0.84	0.87	0.96	0.89	0.85	0.89	0.91	0.95	0.96	0.96	0.96	0.87	0.94
467.15		1.02	0.93	0.85	0.99	0.84	0.97	0.87	0.92	0.96	0.90	0.97	0.94	0.85	0.86	0.96	0.89	0.86	0.89	0.93	0.95	0.96	0.96	0.96	0.86	0.94
467.94		1.02	0.93	0.85	0.99	0.85	0.97	0.87	0.92	0.96	0.90	0.96	0.92	0.84	0.88	0.96	0.91	0.85	0.90	0.93	0.95	0.96	0.96	0.96	0.87	0.95
468.73		1.02	0.93	0.85	0.99	0.85	0.97	0.88	0.92	0.96	0.91	0.96	0.92	0.85	0.88	0.96	0.90	0.86	0.90	0.93	0.95	0.96	0.96	0.96	0.87	0.95

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
469.51		1.02	0.93	0.85	0.99	0.85	0.97	0.88	0.92	0.96	0.91	0.96	0.93	0.83	0.86	0.96	0.90	0.86	0.90	0.92	0.95	0.96	0.96	0.97	0.87	0.95
470.30		1.02	0.93	0.86	0.99	0.85	0.97	0.88	0.93	0.96	0.91	0.96	0.91	0.85	0.87	0.96	0.91	0.86	0.90	0.92	0.95	0.96	0.97	0.96	0.88	0.95
471.09		1.01	0.93	0.85	0.99	0.86	0.97	0.87	0.93	0.97	0.90	0.97	0.92	0.85	0.88	0.96	0.89	0.86	0.90	0.92	0.95	0.96	0.96	0.96	0.87	0.95
471.88		1.01	0.93	0.86	0.99	0.86	0.97	0.88	0.93	0.97	0.90	0.97	0.92	0.85	0.88	0.96	0.89	0.86	0.90	0.92	0.95	0.96	0.97	0.96	0.89	0.95
472.67		1.01	0.93	0.86	0.99	0.86	0.97	0.88	0.93	0.97	0.90	0.96	0.93	0.87	0.87	0.96	0.89	0.86	0.90	0.92	0.95	0.96	0.97	0.96	0.87	0.95
473.46		1.01	0.93	0.86	0.99	0.86	0.97	0.87	0.93	0.97	0.90	0.97	0.92	0.85	0.89	0.96	0.92	0.86	0.90	0.93	0.95	0.96	0.96	0.96	0.88	0.94
474.25		1.01	0.93	0.86	0.99	0.86	0.97	0.88	0.93	0.98	0.90	0.96	0.92	0.87	0.89	0.96	0.90	0.86	0.90	0.92	0.95	0.96	0.96	0.96	0.88	0.94
475.04		1.01	0.93	0.86	0.99	0.86	0.97	0.88	0.93	0.98	0.90	0.96	0.91	0.87	0.89	0.96	0.91	0.86	0.90	0.93	0.95	0.96	0.96	0.96	0.87	0.94
475.83		1.01	0.93	0.86	0.99	0.86	0.97	0.89	0.93	0.97	0.90	0.97	0.92	0.85	0.87	0.96	0.91	0.86	0.90	0.93	0.95	0.96	0.96	0.96	0.88	0.94
476.61		1.02	0.93	0.86	0.99	0.86	0.97	0.87	0.92	0.97	0.90	0.97	0.92	0.85	0.90	0.96	0.91	0.86	0.90	0.93	0.95	0.96	0.96	0.96	0.88	0.94
477.40		1.02	0.93	0.86	0.99	0.86	0.97	0.89	0.93	0.97	0.90	0.97	0.93	0.85	0.89	0.96	0.90	0.86	0.90	0.92	0.95	0.96	0.96	0.97	0.88	0.94
478.19		1.02	0.93	0.86	0.99	0.87	0.97	0.88	0.92	0.97	0.90	0.97	0.94	0.86	0.89	0.96	0.91	0.86	0.90	0.93	0.95	0.96	0.96	0.97	0.88	0.94
478.98		1.02	0.93	0.87	0.99	0.87	0.97	0.88	0.93	0.97	0.90	0.97	0.93	0.87	0.89	0.96	0.89	0.86	0.90	0.92	0.95	0.96	0.95	0.97	0.88	0.94
479.77		1.03	0.93	0.87	0.99	0.87	0.97	0.88	0.93	0.97	0.90	0.97	0.93	0.86	0.90	0.96	0.91	0.87	0.90	0.93	0.95	0.96	0.95	0.97	0.90	0.94
480.56		1.02	0.94	0.87	0.99	0.87	0.97	0.88	0.93	0.97	0.91	0.97	0.92	0.85	0.90	0.96	0.91	0.86	0.90	0.93	0.95	0.97	0.95	0.97	0.89	0.94
481.34		1.02	0.93	0.87	0.99	0.87	0.97	0.88	0.93	0.97	0.90	0.97	0.93	0.87	0.89	0.97	0.91	0.87	0.90	0.93	0.95	0.97	0.95	0.97	0.88	0.94
482.13		1.02	0.93	0.87	0.99	0.87	0.97	0.88	0.93	0.97	0.90	0.97	0.93	0.87	0.90	0.97	0.91	0.87	0.90	0.92	0.95	0.97	0.96	0.97	0.89	0.94
482.92		1.02	0.93	0.87	0.99	0.88	0.97	0.88	0.92	0.97	0.90	0.97	0.94	0.87	0.90	0.97	0.91	0.87	0.91	0.93	0.95	0.97	0.96	0.97	0.89	0.94
483.71		1.02	0.93	0.87	0.99	0.88	0.97	0.88	0.92	0.97	0.90	0.97	0.94	0.86	0.90	0.97	0.91	0.87	0.91	0.93	0.95	0.97	0.96	0.97	0.91	0.94
484.49		1.02	0.93	0.87	0.99	0.88	0.97	0.88	0.92	0.97	0.90	0.97	0.93	0.87	0.90	0.96	0.91	0.87	0.91	0.93	0.95	0.97	0.96	0.97	0.88	0.94
485.28		1.02	0.93	0.88	0.99	0.88	0.97	0.89	0.92	0.97	0.90	0.97	0.93	0.86	0.89	0.96	0.91	0.87	0.91	0.93	0.95	0.97	0.96	0.97	0.89	0.94
486.07		1.02	0.93	0.88	0.99	0.88	0.97	0.88	0.91	0.97	0.90	0.97	0.93	0.87	0.91	0.96	0.91	0.87	0.90	0.94	0.95	0.97	0.96	0.97	0.89	0.94
486.86		1.02	0.93	0.88	0.99	0.88	0.97	0.88	0.91	0.97	0.90	0.97	0.94	0.86	0.91	0.96	0.91	0.87	0.90	0.93	0.96	0.97	0.96	0.97	0.88	0.94
487.64		1.02	0.93	0.88	0.99	0.88	0.97	0.88	0.92	0.97	0.90	0.97	0.93	0.87	0.90	0.96	0.91	0.88	0.90	0.93	0.96	0.96	0.96	0.97	0.90	0.94

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
488.43		1.03	0.94	0.88	0.99	0.88	0.97	0.88	0.91	0.96	0.89	0.98	0.95	0.87	0.91	0.96	0.92	0.87	0.91	0.93	0.96	0.97	0.96	0.98	0.90	0.94
489.22		1.03	0.94	0.88	0.99	0.88	0.97	0.89	0.91	0.96	0.89	0.98	0.93	0.86	0.91	0.97	0.92	0.87	0.92	0.93	0.96	0.97	0.96	0.98	0.90	0.95
490.01		1.03	0.95	0.88	0.99	0.88	0.97	0.88	0.91	0.96	0.90	0.99	0.94	0.86	0.91	0.97	0.92	0.87	0.92	0.94	0.96	0.97	0.96	0.98	0.90	0.95
490.79		1.04	0.95	0.88	0.99	0.88	0.98	0.89	0.91	0.96	0.90	0.99	0.92	0.87	0.91	0.97	0.94	0.87	0.92	0.98	0.96	0.97	0.97	0.98	0.88	0.95
491.58		1.04	0.95	0.88	0.99	0.89	0.98	0.89	0.92	0.96	0.90	0.99	0.94	0.88	0.89	0.97	0.91	0.87	0.92	0.93	0.96	0.97	0.96	0.98	0.90	0.95
492.37		1.04	0.95	0.88	0.99	0.89	0.98	0.89	0.92	0.96	0.90	0.99	0.93	0.87	0.91	0.98	0.91	0.87	0.93	0.93	0.96	0.97	0.96	0.98	0.89	0.95
493.16		1.04	0.95	0.88	0.99	0.89	0.98	0.89	0.92	0.96	0.90	0.99	0.92	0.88	0.90	0.98	0.91	0.87	0.93	0.95	0.96	0.97	0.96	0.98	0.90	0.95
493.94		1.02	0.93	0.88	0.99	0.89	0.98	0.89	0.94	0.98	0.91	0.98	0.93	0.87	0.92	0.97	0.92	0.87	0.91	0.94	0.96	0.97	0.96	0.97	0.90	0.95
494.73		1.02	0.94	0.88	0.99	0.89	0.98	0.89	0.93	0.98	0.91	0.97	0.94	0.87	0.91	0.97	0.92	0.88	0.91	0.94	0.96	0.97	0.96	0.97	0.91	0.95
495.52		1.02	0.94	0.88	0.99	0.89	0.98	0.89	0.93	0.98	0.91	0.97	0.93	0.87	0.93	0.97	0.92	0.88	0.91	0.93	0.96	0.97	0.96	0.97	0.90	0.95
496.30		1.02	0.94	0.88	1.00	0.89	0.97	0.89	0.93	0.98	0.91	0.97	0.93	0.87	0.92	0.97	0.92	0.88	0.91	0.94	0.96	0.97	0.96	0.98	0.91	0.95
497.09		1.02	0.94	0.88	1.00	0.89	0.97	0.89	0.93	0.98	0.92	0.97	0.93	0.88	0.91	0.97	0.92	0.88	0.92	0.94	0.96	0.97	0.96	0.97	0.91	0.95
497.88		1.02	0.94	0.88	1.00	0.89	0.97	0.89	0.93	0.98	0.91	0.97	0.95	0.88	0.92	0.97	0.92	0.87	0.92	0.94	0.96	0.97	0.96	0.97	0.90	0.95
498.66		1.02	0.94	0.89	1.00	0.89	0.97	0.89	0.93	0.97	0.91	0.97	0.94	0.88	0.91	0.96	0.93	0.88	0.92	0.93	0.96	0.97	0.96	0.97	0.90	0.95
499.45		1.02	0.94	0.89	1.00	0.89	0.97	0.90	0.93	0.97	0.91	0.97	0.94	0.87	0.91	0.97	0.92	0.88	0.92	0.94	0.96	0.97	0.96	0.97	0.91	0.95
500.24		1.02	0.94	0.89	1.00	0.89	0.98	0.89	0.93	0.97	0.91	0.97	0.93	0.88	0.91	0.96	0.91	0.88	0.92	0.94	0.96	0.97	0.96	0.97	0.91	0.95
501.02		1.02	0.94	0.89	1.00	0.89	0.98	0.89	0.94	0.97	0.91	0.97	0.94	0.88	0.92	0.96	0.93	0.88	0.92	0.94	0.96	0.97	0.96	0.97	0.91	0.95
501.81		1.02	0.94	0.89	0.99	0.89	0.98	0.89	0.93	0.98	0.91	0.97	0.95	0.88	0.92	0.97	0.92	0.88	0.92	0.94	0.96	0.97	0.96	0.97	0.91	0.95
502.59		1.02	0.94	0.89	0.99	0.89	0.97	0.89	0.93	0.98	0.91	0.97	0.95	0.88	0.92	0.97	0.92	0.88	0.92	0.93	0.96	0.97	0.96	0.97	0.91	0.95
503.38		1.02	0.94	0.89	0.99	0.89	0.98	0.89	0.93	0.98	0.91	0.97	0.93	0.88	0.92	0.97	0.93	0.88	0.92	0.94	0.96	0.97	0.96	0.97	0.91	0.95
504.17		1.02	0.94	0.89	0.99	0.90	0.98	0.89	0.93	0.98	0.91	0.97	0.94	0.89	0.92	0.97	0.93	0.89	0.92	0.94	0.96	0.97	0.96	0.97	0.91	0.95
504.95		1.02	0.94	0.89	0.99	0.90	0.97	0.89	0.93	0.98	0.91	0.97	0.94	0.88	0.93	0.97	0.91	0.88	0.92	0.94	0.96	0.97	0.97	0.98	0.91	0.95
505.74		1.02	0.94	0.89	0.99	0.90	0.97	0.90	0.93	0.98	0.91	0.97	0.94	0.89	0.92	0.97	0.93	0.89	0.92	0.94	0.96	0.97	0.97	0.98	0.91	0.95
506.52		1.02	0.94	0.89	0.99	0.90	0.97	0.89	0.93	0.99	0.91	0.97	0.94	0.87	0.92	0.97	0.93	0.89	0.92	0.94	0.96	0.97	0.97	0.97	0.91	0.95

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
507.31		1.02	0.94	0.89	0.99	0.90	0.97	0.90	0.93	0.98	0.91	0.97	0.94	0.89	0.92	0.96	0.92	0.89	0.92	0.95	0.96	0.97	0.97	0.97	0.91	0.95
508.09		1.02	0.94	0.89	0.99	0.90	0.97	0.89	0.94	0.98	0.91	0.96	0.95	0.89	0.93	0.96	0.93	0.88	0.92	0.95	0.96	0.97	0.97	0.97	0.91	0.95
508.88		1.02	0.94	0.90	1.00	0.90	0.97	0.89	0.94	0.98	0.91	0.96	0.95	0.89	0.92	0.96	0.91	0.89	0.92	0.95	0.96	0.97	0.97	0.97	0.91	0.95
509.67		1.02	0.94	0.90	0.99	0.90	0.97	0.90	0.93	0.99	0.91	0.97	0.94	0.89	0.93	0.96	0.92	0.89	0.92	0.94	0.96	0.97	0.97	0.97	0.91	0.96
510.45		1.02	0.94	0.89	0.99	0.90	0.97	0.89	0.94	0.98	0.91	0.97	0.95	0.90	0.92	0.96	0.92	0.88	0.92	0.94	0.96	0.97	0.97	0.97	0.91	0.96
511.24		1.02	0.94	0.90	0.99	0.90	0.98	0.90	0.94	0.98	0.91	0.97	0.94	0.89	0.92	0.97	0.93	0.89	0.92	0.94	0.96	0.98	0.97	0.97	0.91	0.96
512.02		1.02	0.94	0.89	0.99	0.90	0.98	0.89	0.94	0.98	0.91	0.97	0.94	0.89	0.93	0.97	0.93	0.89	0.93	0.95	0.96	0.97	0.97	0.98	0.91	0.96
512.81		1.02	0.94	0.90	1.00	0.90	0.98	0.89	0.94	0.98	0.91	0.97	0.95	0.89	0.92	0.97	0.93	0.89	0.93	0.95	0.96	0.98	0.97	0.98	0.91	0.96
513.59		1.02	0.94	0.90	0.99	0.90	0.98	0.90	0.94	0.99	0.91	0.97	0.95	0.88	0.93	0.97	0.93	0.89	0.92	0.94	0.96	0.98	0.97	0.97	0.91	0.96
514.38		1.02	0.94	0.90	0.99	0.90	0.98	0.90	0.94	0.99	0.91	0.98	0.95	0.89	0.92	0.97	0.93	0.89	0.92	0.94	0.96	0.98	0.97	0.98	0.91	0.96
515.16		1.02	0.95	0.90	1.00	0.90	0.98	0.90	0.95	0.99	0.91	0.97	0.95	0.89	0.93	0.97	0.93	0.89	0.92	0.94	0.96	0.98	0.97	0.98	0.91	0.96
515.95		1.02	0.95	0.90	1.00	0.90	0.98	0.90	0.95	0.99	0.91	0.97	0.94	0.88	0.92	0.97	0.93	0.89	0.93	0.94	0.96	0.98	0.96	0.98	0.91	0.96
516.73		1.02	0.95	0.90	1.00	0.90	0.98	0.89	0.95	0.99	0.91	0.97	0.94	0.90	0.93	0.97	0.92	0.89	0.92	0.94	0.96	0.97	0.96	0.98	0.91	0.96
517.52		1.02	0.95	0.90	1.00	0.90	0.98	0.89	0.95	0.99	0.91	0.97	0.95	0.89	0.92	0.97	0.93	0.89	0.92	0.94	0.96	0.98	0.96	0.98	0.91	0.96
518.30		1.02	0.94	0.90	0.99	0.90	0.98	0.90	0.95	0.99	0.91	0.97	0.94	0.90	0.93	0.97	0.93	0.90	0.92	0.94	0.96	0.97	0.96	0.98	0.91	0.96
519.09		1.02	0.95	0.90	0.99	0.90	0.98	0.90	0.95	0.99	0.92	0.97	0.94	0.89	0.93	0.97	0.93	0.89	0.92	0.95	0.96	0.97	0.96	0.98	0.90	0.96
519.87		1.02	0.95	0.90	0.99	0.90	0.98	0.90	0.95	0.99	0.92	0.97	0.94	0.90	0.92	0.97	0.93	0.89	0.92	0.95	0.96	0.97	0.96	0.98	0.93	0.96
520.65		1.03	0.94	0.90	0.99	0.90	0.98	0.89	0.95	0.99	0.92	0.98	0.95	0.89	0.92	0.97	0.93	0.90	0.92	0.94	0.96	0.97	0.96	0.98	0.92	0.96
521.44		1.02	0.95	0.90	1.00	0.90	0.98	0.90	0.94	0.99	0.92	0.98	0.94	0.89	0.92	0.97	0.93	0.89	0.92	0.94	0.96	0.97	0.96	0.98	0.91	0.96
522.22		1.02	0.95	0.90	1.00	0.90	0.98	0.89	0.94	0.99	0.92	0.98	0.96	0.88	0.93	0.97	0.94	0.89	0.92	0.95	0.96	0.97	0.96	0.98	0.91	0.96
523.01		1.03	0.94	0.90	1.00	0.89	0.98	0.90	0.94	0.98	0.92	0.98	0.94	0.89	0.93	0.97	0.93	0.90	0.92	0.95	0.96	0.97	0.96	0.98	0.91	0.96
523.79		1.03	0.94	0.90	1.00	0.89	0.98	0.90	0.95	0.98	0.92	0.98	0.94	0.90	0.93	0.97	0.93	0.89	0.92	0.95	0.96	0.98	0.97	0.98	0.91	0.96
524.58		1.02	0.94	0.91	1.00	0.89	0.98	0.90	0.95	0.99	0.92	0.98	0.95	0.89	0.93	0.97	0.93	0.89	0.93	0.95	0.96	0.97	0.96	0.98	0.91	0.96
525.36		1.03	0.94	0.91	1.00	0.89	0.98	0.90	0.95	0.99	0.93	0.98	0.95	0.89	0.93	0.97	0.93	0.89	0.93	0.95	0.96	0.98	0.97	0.98	0.91	0.96

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
526.14		1.02	0.94	0.91	1.00	0.89	0.98	0.90	0.95	0.99	0.93	0.98	0.94	0.89	0.92	0.97	0.93	0.89	0.93	0.95	0.96	0.98	0.97	0.98	0.91	0.96
526.93		1.02	0.94	0.91	1.00	0.89	0.98	0.90	0.95	0.99	0.93	0.97	0.95	0.89	0.93	0.97	0.93	0.90	0.93	0.94	0.96	0.98	0.97	0.98	0.91	0.96
527.71		1.02	0.94	0.90	1.00	0.88	0.98	0.90	0.95	0.99	0.93	0.97	0.95	0.89	0.92	0.97	0.94	0.90	0.93	0.95	0.96	0.98	0.97	0.98	0.91	0.96
528.50		1.02	0.94	0.90	1.00	0.88	0.98	0.90	0.95	0.99	0.92	0.98	0.94	0.89	0.93	0.97	0.93	0.90	0.93	0.95	0.96	0.98	0.97	0.98	0.91	0.96
529.28		1.02	0.94	0.90	1.00	0.88	0.98	0.90	0.94	0.99	0.92	0.98	0.95	0.89	0.93	0.97	0.94	0.90	0.93	0.95	0.96	0.98	0.97	0.98	0.90	0.96
530.06		1.02	0.94	0.90	1.00	0.88	0.98	0.90	0.95	0.99	0.92	0.97	0.95	0.89	0.92	0.97	0.93	0.90	0.93	0.95	0.96	0.98	0.97	0.98	0.91	0.96
530.85		1.02	0.93	0.90	1.00	0.88	0.98	0.90	0.94	0.99	0.92	0.97	0.95	0.88	0.93	0.97	0.94	0.90	0.93	0.95	0.96	0.98	0.97	0.98	0.91	0.96
531.63		1.02	0.93	0.91	1.00	0.88	0.98	0.90	0.94	0.99	0.92	0.98	0.95	0.89	0.93	0.98	0.94	0.90	0.93	0.95	0.97	0.98	0.97	0.98	0.90	0.96
532.41		1.02	0.93	0.91	1.00	0.88	0.98	0.90	0.94	0.98	0.92	0.98	0.95	0.89	0.94	0.97	0.94	0.90	0.93	0.95	0.97	0.98	0.97	0.98	0.90	0.96
533.20		1.02	0.93	0.91	1.00	0.87	0.98	0.90	0.94	0.98	0.92	0.98	0.95	0.89	0.92	0.97	0.94	0.90	0.93	0.94	0.97	0.98	0.97	0.97	0.90	0.96
533.98		1.02	0.93	0.91	1.00	0.87	0.98	0.90	0.94	0.98	0.92	0.97	0.95	0.88	0.93	0.97	0.94	0.90	0.93	0.95	0.97	0.98	0.97	0.98	0.90	0.96
534.76		1.02	0.93	0.91	1.00	0.87	0.98	0.90	0.95	0.98	0.92	0.97	0.95	0.89	0.92	0.97	0.94	0.90	0.93	0.95	0.97	0.98	0.97	0.98	0.89	0.96
535.55		1.02	0.93	0.91	1.00	0.87	0.98	0.90	0.94	0.98	0.92	0.97	0.94	0.88	0.93	0.97	0.94	0.90	0.93	0.95	0.97	0.98	0.97	0.97	0.90	0.96
536.33		1.02	0.93	0.91	1.00	0.87	0.98	0.90	0.94	0.98	0.92	0.97	0.95	0.89	0.92	0.97	0.94	0.90	0.93	0.96	0.97	0.98	0.97	0.98	0.90	0.96
537.11		1.02	0.93	0.91	1.00	0.87	0.98	0.90	0.94	0.99	0.92	0.97	0.95	0.88	0.93	0.97	0.94	0.90	0.93	0.95	0.97	0.97	0.97	0.98	0.90	0.96
537.90		1.02	0.93	0.91	1.00	0.87	0.98	0.90	0.95	0.99	0.92	0.97	0.94	0.89	0.92	0.97	0.93	0.90	0.93	0.95	0.97	0.97	0.97	0.98	0.90	0.96
538.68		1.03	0.93	0.91	1.00	0.87	0.98	0.90	0.95	0.99	0.92	0.98	0.95	0.88	0.92	0.97	0.94	0.91	0.93	0.95	0.97	0.97	0.97	0.98	0.90	0.96
539.46		1.03	0.93	0.91	1.00	0.87	0.98	0.90	0.95	0.99	0.92	0.98	0.95	0.88	0.93	0.98	0.94	0.90	0.93	0.96	0.97	0.98	0.97	0.98	0.89	0.96
540.24		1.03	0.93	0.91	1.00	0.87	0.98	0.91	0.95	0.99	0.92	0.98	0.94	0.89	0.92	0.98	0.94	0.91	0.93	0.95	0.97	0.97	0.97	0.98	0.89	0.96
541.03		1.03	0.93	0.91	1.00	0.87	0.98	0.90	0.95	0.98	0.92	0.98	0.94	0.89	0.93	0.98	0.94	0.90	0.93	0.95	0.97	0.97	0.98	0.98	0.90	0.96
541.81		1.03	0.93	0.91	1.00	0.86	0.98	0.90	0.95	0.98	0.92	0.98	0.95	0.89	0.92	0.98	0.95	0.91	0.93	0.95	0.97	0.98	0.98	0.98	0.89	0.96
542.59		1.03	0.93	0.91	1.00	0.86	0.98	0.90	0.95	0.98	0.92	0.98	0.95	0.88	0.92	0.98	0.94	0.91	0.92	0.95	0.97	0.98	0.98	0.98	0.90	0.96
543.37		1.02	0.93	0.91	1.00	0.87	0.98	0.90	0.95	0.98	0.92	0.98	0.95	0.89	0.93	0.98	0.94	0.90	0.92	0.95	0.97	0.98	0.98	0.98	0.90	0.96
544.16		1.03	0.93	0.91	1.00	0.87	0.98	0.90	0.95	0.98	0.92	0.98	0.95	0.89	0.92	0.98	0.94	0.91	0.92	0.95	0.97	0.98	0.98	0.98	0.90	0.96

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
544.94		1.02	0.93	0.92	1.00	0.87	0.98	0.90	0.95	0.98	0.92	0.98	0.94	0.88	0.93	0.98	0.93	0.90	0.92	0.95	0.97	0.98	0.98	0.98	0.90	0.96
545.72		1.02	0.93	0.92	1.00	0.87	0.98	0.90	0.95	0.99	0.92	0.98	0.94	0.89	0.92	0.98	0.94	0.91	0.93	0.95	0.97	0.98	0.98	0.98	0.90	0.96
546.50		1.03	0.93	0.92	1.00	0.87	0.98	0.90	0.95	0.99	0.92	0.97	0.95	0.89	0.92	0.98	0.95	0.91	0.93	0.95	0.97	0.98	0.98	0.98	0.89	0.96
547.28		1.03	0.93	0.92	1.00	0.87	0.98	0.90	0.95	0.99	0.92	0.98	0.95	0.89	0.92	0.98	0.94	0.91	0.93	0.96	0.97	0.98	0.97	0.98	0.89	0.96
548.07		1.03	0.93	0.92	1.00	0.87	0.98	0.90	0.95	0.99	0.92	0.98	0.95	0.89	0.92	0.98	0.95	0.91	0.93	0.95	0.97	0.98	0.97	0.98	0.90	0.96
548.85		1.03	0.93	0.92	1.00	0.87	0.98	0.90	0.95	0.99	0.92	0.98	0.95	0.89	0.93	0.98	0.94	0.91	0.93	0.95	0.97	0.98	0.97	0.98	0.90	0.96
549.63		1.02	0.93	0.92	1.00	0.88	0.98	0.90	0.95	0.99	0.92	0.98	0.95	0.89	0.93	0.98	0.94	0.91	0.93	0.95	0.97	0.98	0.97	0.98	0.89	0.96
550.41		1.02	0.93	0.92	1.00	0.88	0.98	0.91	0.95	0.99	0.92	0.98	0.95	0.89	0.93	0.98	0.95	0.91	0.93	0.96	0.97	0.98	0.97	0.98	0.90	0.96
551.19		1.02	0.94	0.92	1.00	0.88	0.98	0.91	0.95	0.99	0.93	0.98	0.95	0.89	0.92	0.98	0.95	0.91	0.93	0.96	0.97	0.98	0.98	0.98	0.90	0.96
551.97		1.02	0.94	0.92	1.00	0.88	0.98	0.90	0.95	0.99	0.92	0.98	0.95	0.90	0.93	0.98	0.94	0.91	0.93	0.95	0.97	0.98	0.98	0.98	0.90	0.96
552.76		1.02	0.94	0.92	1.00	0.89	0.98	0.90	0.95	0.99	0.92	0.98	0.95	0.90	0.93	0.98	0.95	0.92	0.93	0.96	0.97	0.98	0.98	0.98	0.90	0.96
553.54		1.02	0.94	0.92	1.00	0.89	0.98	0.90	0.94	0.99	0.92	0.98	0.95	0.90	0.93	0.97	0.94	0.91	0.93	0.95	0.97	0.98	0.98	0.99	0.90	0.96
554.32		1.02	0.94	0.92	1.00	0.89	0.98	0.90	0.94	0.99	0.92	0.98	0.95	0.90	0.93	0.98	0.93	0.91	0.93	0.96	0.97	0.98	0.98	0.99	0.91	0.96
555.10		1.02	0.95	0.92	1.00	0.89	0.98	0.90	0.94	0.99	0.92	0.98	0.95	0.90	0.93	0.97	0.94	0.91	0.93	0.96	0.97	0.98	0.98	0.99	0.91	0.96
555.88		1.02	0.95	0.92	1.00	0.89	0.98	0.90	0.94	0.99	0.92	0.98	0.95	0.90	0.93	0.97	0.95	0.92	0.93	0.95	0.97	0.98	0.98	0.99	0.91	0.96
556.66		1.02	0.95	0.92	1.00	0.90	0.98	0.91	0.94	0.99	0.92	0.98	0.95	0.90	0.93	0.97	0.94	0.91	0.93	0.96	0.97	0.98	0.98	0.98	0.91	0.96
557.44		1.01	0.95	0.92	1.00	0.90	0.98	0.90	0.94	0.99	0.92	0.98	0.95	0.90	0.93	0.97	0.94	0.92	0.93	0.95	0.97	0.98	0.98	0.98	0.91	0.96
558.23		1.01	0.94	0.92	1.00	0.90	0.98	0.91	0.94	0.99	0.92	0.98	0.96	0.90	0.93	0.97	0.94	0.92	0.93	0.95	0.97	0.98	0.98	0.98	0.91	0.96
559.01		1.01	0.94	0.92	1.00	0.90	0.98	0.91	0.94	0.99	0.92	0.98	0.95	0.91	0.94	0.98	0.95	0.91	0.93	0.95	0.97	0.98	0.98	0.98	0.91	0.96
559.79		1.01	0.94	0.92	1.01	0.90	0.98	0.91	0.94	0.99	0.92	0.98	0.95	0.91	0.94	0.97	0.95	0.92	0.93	0.96	0.97	0.98	0.98	0.98	0.90	0.96
560.57		1.01	0.94	0.92	1.01	0.90	0.98	0.91	0.94	0.99	0.92	0.98	0.95	0.91	0.93	0.98	0.95	0.92	0.94	0.95	0.97	0.98	0.98	0.98	0.91	0.96
561.35		1.01	0.94	0.92	1.01	0.90	0.98	0.91	0.94	0.99	0.92	0.98	0.95	0.90	0.94	0.98	0.94	0.92	0.94	0.96	0.97	0.98	0.98	0.98	0.92	0.96
562.13		1.01	0.94	0.92	1.00	0.90	0.98	0.91	0.94	0.99	0.92	0.98	0.96	0.91	0.94	0.98	0.94	0.92	0.94	0.96	0.97	0.98	0.98	0.98	0.91	0.96
562.91		1.01	0.94	0.92	1.01	0.90	0.98	0.91	0.94	0.99	0.91	0.97	0.95	0.91	0.93	0.98	0.95	0.92	0.94	0.96	0.97	0.98	0.98	0.98	0.91	0.96

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
563.69		1.01	0.94	0.92	1.01	0.90	0.98	0.91	0.94	0.99	0.92	0.97	0.96	0.91	0.94	0.97	0.95	0.92	0.94	0.96	0.97	0.98	0.97	0.98	0.91	0.96
564.47		1.01	0.94	0.92	1.01	0.90	0.99	0.91	0.94	0.99	0.92	0.98	0.96	0.91	0.94	0.97	0.95	0.92	0.94	0.96	0.97	0.98	0.98	0.98	0.92	0.96
565.25		1.01	0.94	0.92	1.01	0.90	0.99	0.91	0.94	0.99	0.92	0.98	0.95	0.91	0.94	0.97	0.95	0.92	0.94	0.96	0.97	0.98	0.97	0.98	0.92	0.96
566.03		1.01	0.94	0.92	1.01	0.89	0.99	0.91	0.95	0.98	0.91	0.98	0.95	0.90	0.94	0.97	0.95	0.92	0.93	0.96	0.96	0.98	0.97	0.98	0.91	0.96
566.81		1.01	0.94	0.92	1.00	0.89	0.99	0.91	0.95	0.98	0.91	0.98	0.96	0.90	0.93	0.97	0.95	0.92	0.93	0.96	0.96	0.98	0.97	0.98	0.91	0.96
567.59		1.01	0.94	0.92	1.00	0.89	0.99	0.91	0.94	0.98	0.91	0.98	0.95	0.91	0.93	0.97	0.95	0.92	0.93	0.96	0.97	0.98	0.97	0.98	0.90	0.96
568.37		1.01	0.94	0.92	1.00	0.89	0.98	0.91	0.94	0.98	0.91	0.98	0.95	0.91	0.93	0.97	0.95	0.92	0.93	0.96	0.97	0.98	0.97	0.98	0.91	0.96
569.15		1.01	0.94	0.92	1.00	0.89	0.98	0.91	0.94	0.98	0.91	0.98	0.95	0.91	0.93	0.97	0.95	0.92	0.93	0.95	0.97	0.98	0.97	0.98	0.91	0.95
569.93		1.01	0.94	0.92	1.00	0.88	0.98	0.91	0.94	0.98	0.91	0.98	0.95	0.91	0.93	0.97	0.95	0.92	0.93	0.96	0.97	0.98	0.97	0.98	0.91	0.95
570.71		1.01	0.93	0.92	1.00	0.88	0.98	0.91	0.94	0.98	0.91	0.98	0.96	0.90	0.94	0.97	0.95	0.92	0.93	0.96	0.97	0.98	0.97	0.98	0.90	0.95
571.49		1.01	0.93	0.92	1.00	0.88	0.98	0.91	0.93	0.98	0.91	0.98	0.95	0.90	0.93	0.97	0.94	0.92	0.93	0.96	0.97	0.98	0.97	0.98	0.91	0.95
572.27		1.01	0.93	0.92	1.00	0.88	0.98	0.91	0.93	0.98	0.91	0.98	0.95	0.90	0.94	0.97	0.95	0.92	0.93	0.96	0.97	0.98	0.97	0.98	0.90	0.95
573.05		1.01	0.93	0.92	1.00	0.88	0.98	0.91	0.93	0.98	0.90	0.98	0.95	0.90	0.93	0.97	0.95	0.92	0.93	0.96	0.97	0.99	0.97	0.98	0.90	0.95
573.83		1.01	0.93	0.92	1.00	0.88	0.98	0.91	0.93	0.98	0.90	0.98	0.95	0.90	0.94	0.97	0.95	0.93	0.93	0.96	0.97	0.99	0.97	0.98	0.90	0.95
574.61		1.01	0.93	0.93	1.00	0.88	0.98	0.91	0.93	0.98	0.90	0.98	0.95	0.90	0.93	0.97	0.95	0.92	0.93	0.96	0.97	0.99	0.97	0.98	0.90	0.95
575.39		1.01	0.93	0.93	1.00	0.88	0.98	0.91	0.93	0.98	0.90	0.98	0.95	0.90	0.93	0.97	0.95	0.92	0.93	0.97	0.97	0.99	0.97	0.98	0.90	0.95
576.17		1.01	0.93	0.93	1.00	0.88	0.98	0.91	0.93	0.98	0.90	0.98	0.95	0.90	0.93	0.97	0.95	0.93	0.93	0.96	0.97	0.99	0.97	0.98	0.90	0.95
576.95		1.01	0.93	0.93	1.00	0.88	0.99	0.91	0.93	0.98	0.90	0.98	0.95	0.90	0.93	0.97	0.95	0.93	0.93	0.96	0.97	0.99	0.97	0.98	0.90	0.95
577.73		1.01	0.93	0.92	1.00	0.88	0.99	0.91	0.93	0.98	0.90	0.98	0.95	0.90	0.93	0.97	0.95	0.93	0.93	0.96	0.97	0.99	0.97	0.98	0.90	0.95
578.51		1.01	0.93	0.93	1.00	0.88	0.99	0.91	0.93	0.98	0.90	0.98	0.95	0.90	0.93	0.97	0.95	0.93	0.93	0.96	0.97	0.98	0.97	0.98	0.90	0.95
579.29		1.01	0.93	0.93	1.00	0.88	0.99	0.91	0.93	0.98	0.90	0.98	0.95	0.90	0.93	0.97	0.95	0.93	0.93	0.96	0.97	0.98	0.97	0.98	0.89	0.95
580.07		1.01	0.93	0.93	1.00	0.88	0.99	0.91	0.93	0.98	0.91	0.98	0.95	0.90	0.93	0.97	0.95	0.93	0.93	0.96	0.97	0.98	0.97	0.98	0.90	0.95
580.84		1.01	0.94	0.93	1.00	0.89	0.99	0.91	0.93	0.98	0.91	0.98	0.95	0.90	0.93	0.97	0.95	0.93	0.93	0.96	0.97	0.99	0.97	0.98	0.90	0.95
581.62		1.01	0.94	0.93	1.00	0.89	0.99	0.91	0.93	0.98	0.91	0.98	0.95	0.90	0.94	0.97	0.95	0.93	0.93	0.96	0.97	0.99	0.97	0.98	0.90	0.95

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
582.40		1.01	0.94	0.93	1.00	0.89	0.98	0.91	0.93	0.98	0.91	0.98	0.95	0.91	0.93	0.97	0.95	0.93	0.93	0.96	0.97	0.99	0.97	0.98	0.91	0.95
583.18		1.01	0.94	0.93	1.00	0.90	0.99	0.91	0.93	0.98	0.91	0.98	0.96	0.91	0.93	0.97	0.95	0.93	0.93	0.96	0.97	0.99	0.98	0.98	0.91	0.95
583.96		1.01	0.94	0.93	1.00	0.90	0.99	0.91	0.93	0.98	0.91	0.98	0.95	0.91	0.93	0.98	0.95	0.93	0.93	0.96	0.97	0.99	0.97	0.98	0.91	0.95
584.74		1.01	0.94	0.93	1.00	0.91	0.99	0.91	0.93	0.98	0.91	0.98	0.96	0.92	0.93	0.98	0.95	0.93	0.93	0.96	0.97	0.99	0.98	0.98	0.91	0.95
585.52		1.01	0.95	0.93	1.00	0.91	0.99	0.91	0.93	0.98	0.91	0.98	0.96	0.92	0.94	0.98	0.95	0.93	0.93	0.96	0.97	0.99	0.98	0.98	0.91	0.95
586.29		1.01	0.95	0.93	1.00	0.92	0.99	0.91	0.93	0.98	0.91	0.98	0.96	0.92	0.94	0.98	0.95	0.93	0.93	0.96	0.97	0.99	0.98	0.98	0.92	0.95
587.07		1.01	0.95	0.93	1.00	0.92	0.99	0.91	0.94	0.98	0.91	0.98	0.96	0.92	0.94	0.98	0.96	0.93	0.93	0.96	0.97	0.99	0.98	0.98	0.92	0.95
587.85		1.01	0.95	0.93	1.00	0.92	0.99	0.91	0.94	0.98	0.91	0.98	0.95	0.92	0.94	0.98	0.95	0.93	0.93	0.97	0.97	0.98	0.98	0.98	0.92	0.95
588.63		1.01	0.95	0.93	1.00	0.93	0.99	0.91	0.94	0.98	0.91	0.98	0.96	0.92	0.94	0.98	0.96	0.94	0.93	0.97	0.97	0.99	0.97	0.98	0.92	0.95
589.41		1.01	0.96	0.93	1.00	0.93	0.99	0.91	0.94	0.98	0.91	0.98	0.96	0.92	0.94	0.98	0.96	0.93	0.93	0.96	0.97	0.99	0.97	0.98	0.93	0.95
590.19		1.01	0.96	0.93	1.00	0.93	0.99	0.92	0.94	0.98	0.91	0.98	0.96	0.93	0.95	0.98	0.96	0.93	0.93	0.96	0.97	0.99	0.97	0.98	0.92	0.95
590.96		1.01	0.96	0.93	1.00	0.94	0.99	0.91	0.94	0.98	0.91	0.98	0.96	0.93	0.95	0.98	0.95	0.93	0.93	0.97	0.97	0.99	0.97	0.98	0.93	0.96
591.74		1.01	0.96	0.93	1.01	0.94	0.99	0.92	0.94	0.98	0.91	0.98	0.96	0.93	0.95	0.98	0.95	0.94	0.93	0.96	0.97	0.99	0.97	0.98	0.92	0.96
592.52		1.01	0.96	0.93	1.00	0.94	0.99	0.91	0.94	0.98	0.91	0.98	0.96	0.93	0.95	0.98	0.95	0.94	0.93	0.97	0.97	0.99	0.97	0.98	0.93	0.96
593.30		1.01	0.96	0.93	1.00	0.94	0.99	0.92	0.94	0.99	0.91	0.98	0.96	0.93	0.95	0.98	0.95	0.94	0.93	0.96	0.97	0.99	0.97	0.98	0.93	0.96
594.08		1.01	0.96	0.93	1.00	0.94	0.99	0.92	0.94	0.99	0.91	0.98	0.96	0.93	0.94	0.99	0.95	0.94	0.94	0.97	0.97	0.99	0.97	0.98	0.93	0.96
594.85		1.01	0.96	0.93	1.01	0.94	0.99	0.91	0.94	0.99	0.91	0.98	0.96	0.93	0.95	0.99	0.96	0.94	0.94	0.97	0.97	0.99	0.97	0.98	0.93	0.96
595.63		1.01	0.96	0.93	1.01	0.95	0.99	0.92	0.94	0.99	0.91	0.98	0.96	0.94	0.95	0.99	0.96	0.94	0.94	0.96	0.98	0.99	0.98	0.98	0.94	0.96
596.41		1.01	0.96	0.93	1.01	0.95	0.99	0.92	0.94	0.99	0.91	0.98	0.96	0.93	0.95	0.99	0.96	0.94	0.94	0.96	0.98	0.99	0.98	0.98	0.93	0.96
597.19		1.01	0.96	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.93	0.95	0.99	0.95	0.94	0.94	0.97	0.98	0.99	0.98	0.98	0.93	0.96
597.96		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.95	0.99	0.96	0.94	0.94	0.97	0.97	0.99	0.98	0.98	0.93	0.96
598.74		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.95	0.99	0.96	0.94	0.94	0.97	0.97	0.99	0.98	0.99	0.93	0.96
599.52		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.96	0.99	0.95	0.94	0.94	0.97	0.97	0.99	0.98	0.99	0.93	0.96
600.29		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.96	0.99	0.96	0.94	0.94	0.97	0.98	0.99	0.97	0.99	0.94	0.96

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
601.07		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.95	0.99	0.96	0.94	0.94	0.97	0.98	0.99	0.97	0.99	0.94	0.96
601.85		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.95	0.98	0.96	0.94	0.94	0.97	0.98	0.99	0.97	0.99	0.94	0.96
602.63		1.01	0.97	0.94	1.01	0.95	0.99	0.91	0.94	0.99	0.92	0.98	0.96	0.93	0.96	0.98	0.96	0.94	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
603.40		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.95	0.98	0.96	0.94	0.94	0.97	0.98	0.99	0.97	0.99	0.94	0.96
604.18		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.95	0.98	0.96	0.94	0.94	0.96	0.98	0.99	0.98	0.99	0.94	0.96
604.96		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.95	0.98	0.96	0.94	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
605.73		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.95	0.98	0.96	0.94	0.94	0.97	0.98	0.99	0.98	0.99	0.93	0.96
606.51		1.01	0.97	0.94	1.01	0.95	0.99	0.91	0.94	0.99	0.92	0.98	0.96	0.94	0.96	0.99	0.96	0.94	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
607.29		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.95	0.99	0.96	0.94	0.94	0.96	0.98	0.99	0.98	0.99	0.93	0.96
608.06		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.95	0.99	0.96	0.94	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
608.84		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.95	0.99	0.95	0.94	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
609.62		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.96	0.99	0.96	0.95	0.94	0.96	0.98	0.99	0.98	0.99	0.94	0.96
610.39		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.95	0.99	0.92	0.98	0.96	0.94	0.96	0.99	0.96	0.95	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
611.17		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.95	0.99	0.92	0.98	0.97	0.94	0.95	0.99	0.96	0.95	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
611.94		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.95	0.99	0.93	0.98	0.97	0.94	0.96	0.99	0.96	0.95	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
612.72		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.95	0.99	0.93	0.98	0.96	0.94	0.96	0.99	0.97	0.95	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
613.50		1.01	0.97	0.95	1.01	0.95	0.99	0.92	0.94	0.99	0.92	0.98	0.96	0.94	0.96	0.99	0.96	0.95	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
614.27		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.94	0.99	0.93	0.98	0.96	0.94	0.96	0.99	0.96	0.95	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
615.05		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.95	0.99	0.93	0.98	0.96	0.94	0.96	0.99	0.96	0.95	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
615.82		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.95	0.99	0.93	0.98	0.97	0.94	0.96	0.99	0.96	0.95	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
616.60		1.01	0.97	0.94	1.01	0.95	0.99	0.92	0.95	0.99	0.93	0.98	0.97	0.95	0.96	0.99	0.96	0.95	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
617.37		1.01	0.97	0.95	1.01	0.94	0.99	0.92	0.95	0.99	0.93	0.98	0.96	0.94	0.96	0.99	0.96	0.95	0.94	0.97	0.98	0.99	0.98	0.99	0.93	0.96
618.15		1.01	0.97	0.95	1.01	0.94	0.99	0.93	0.95	0.99	0.93	0.98	0.97	0.94	0.95	0.99	0.96	0.95	0.94	0.97	0.98	0.99	0.98	0.99	0.94	0.96
618.93		1.01	0.97	0.95	1.01	0.94	0.99	0.92	0.95	0.99	0.93	0.98	0.97	0.94	0.96	0.99	0.96	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.96

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
619.70		1.01	0.97	0.95	1.01	0.94	0.99	0.92	0.95	0.99	0.93	0.98	0.96	0.95	0.96	0.99	0.96	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.96
620.48		1.01	0.97	0.95	1.01	0.94	0.99	0.92	0.95	0.99	0.93	0.98	0.96	0.95	0.96	0.99	0.96	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.96
621.25		1.01	0.97	0.95	1.01	0.95	0.99	0.92	0.95	0.99	0.94	0.98	0.96	0.95	0.96	0.99	0.96	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.96
622.03		1.01	0.97	0.95	1.01	0.95	0.99	0.92	0.95	0.99	0.94	0.98	0.96	0.95	0.96	0.99	0.97	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.96
622.80		1.01	0.97	0.95	1.01	0.95	0.99	0.92	0.95	0.99	0.94	0.99	0.96	0.95	0.96	0.99	0.97	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.96
623.58		1.01	0.97	0.95	1.01	0.95	0.99	0.92	0.95	0.99	0.94	0.99	0.97	0.95	0.96	0.99	0.96	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.96
624.35		1.01	0.97	0.95	1.01	0.95	0.99	0.92	0.95	0.99	0.94	0.99	0.96	0.95	0.96	0.99	0.96	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.97
625.13		1.01	0.97	0.95	1.01	0.95	0.99	0.92	0.96	1.00	0.94	0.99	0.97	0.95	0.96	0.99	0.97	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.97
625.90		1.01	0.97	0.95	1.01	0.95	0.99	0.93	0.96	1.00	0.94	0.98	0.97	0.95	0.96	0.99	0.97	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.97
626.68		1.01	0.97	0.95	1.01	0.95	0.99	0.93	0.96	1.00	0.94	0.99	0.97	0.95	0.96	0.99	0.97	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.97
627.45		1.01	0.97	0.95	1.01	0.95	0.99	0.92	0.96	1.00	0.94	0.99	0.96	0.95	0.96	0.99	0.97	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.97
628.22		1.01	0.97	0.95	1.01	0.95	0.99	0.92	0.96	1.00	0.94	0.98	0.97	0.95	0.96	0.99	0.97	0.96	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.97
629.00		1.02	0.97	0.95	1.01	0.96	0.99	0.92	0.96	1.00	0.94	0.99	0.97	0.95	0.96	0.99	0.97	0.95	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.97
629.77		1.02	0.97	0.95	1.01	0.96	0.99	0.93	0.96	1.00	0.94	0.98	0.97	0.95	0.96	0.99	0.97	0.96	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.97
630.55		1.02	0.97	0.95	1.01	0.96	0.99	0.93	0.96	1.00	0.94	0.99	0.97	0.95	0.96	0.99	0.96	0.96	0.95	0.98	0.98	0.99	0.98	0.99	0.95	0.97
631.32		1.02	0.97	0.95	1.01	0.96	0.99	0.93	0.96	1.00	0.94	0.99	0.97	0.95	0.96	0.99	0.97	0.96	0.95	0.97	0.98	0.99	0.98	0.99	0.94	0.97
632.10		1.02	0.97	0.95	1.01	0.96	0.99	0.93	0.96	1.00	0.94	0.99	0.97	0.95	0.96	0.99	0.97	0.96	0.95	0.98	0.98	0.99	0.98	0.99	0.95	0.97
632.87		1.02	0.97	0.95	1.01	0.96	0.99	0.93	0.97	1.00	0.94	0.99	0.97	0.95	0.96	0.99	0.96	0.96	0.95	0.97	0.98	0.99	0.98	0.99	0.95	0.97
633.65		1.02	0.97	0.95	1.01	0.96	0.99	0.93	0.97	1.00	0.95	0.99	0.97	0.95	0.96	0.99	0.97	0.96	0.95	0.97	0.98	0.99	0.99	0.99	0.94	0.98
634.42		1.02	0.97	0.95	1.01	0.97	0.99	0.93	0.97	1.00	0.95	0.99	0.97	0.95	0.96	0.99	0.97	0.96	0.95	0.97	0.98	0.99	0.99	0.99	0.94	0.98
635.19		1.02	0.97	0.95	1.01	0.97	0.99	0.93	0.97	1.00	0.95	0.99	0.97	0.95	0.96	0.99	0.98	0.95	0.95	0.98	0.98	0.99	0.99	0.99	0.94	0.98
635.97		1.02	0.98	0.95	1.01	0.97	0.99	0.93	0.97	1.00	0.95	0.99	0.97	0.95	0.96	0.99	0.97	0.96	0.95	0.98	0.98	0.99	0.98	0.99	0.94	0.98
636.74		1.02	0.98	0.95	1.01	0.97	0.99	0.93	0.97	1.00	0.95	0.99	0.97	0.95	0.96	0.99	0.97	0.96	0.95	0.98	0.98	0.99	0.98	0.99	0.95	0.98
637.51		1.01	0.98	0.95	1.01	0.97	0.99	0.93	0.97	1.00	0.95	0.98	0.97	0.95	0.96	0.99	0.97	0.96	0.96	0.98	0.98	0.99	0.98	0.99	0.94	0.98

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
638.29		1.02	0.98	0.96	1.01	0.97	0.99	0.93	0.97	0.99	0.95	0.99	0.97	0.96	0.96	0.99	0.97	0.96	0.96	0.98	0.98	0.99	0.99	0.99	0.95	0.98
639.06		1.02	0.98	0.96	1.01	0.97	0.99	0.92	0.97	0.99	0.95	0.99	0.97	0.95	0.97	0.99	0.96	0.96	0.96	0.98	0.98	0.99	0.98	0.99	0.95	0.98
639.84		1.02	0.98	0.95	1.01	0.97	0.99	0.93	0.97	0.99	0.95	0.98	0.97	0.95	0.97	0.99	0.97	0.96	0.96	0.98	0.98	0.99	0.98	0.99	0.95	0.98
640.61		1.02	0.98	0.96	1.01	0.97	0.99	0.93	0.97	0.99	0.96	0.98	0.97	0.96	0.97	0.99	0.97	0.96	0.96	0.97	0.98	0.99	0.98	0.99	0.95	0.98
641.38		1.02	0.98	0.96	1.01	0.97	0.99	0.93	0.97	0.99	0.96	0.98	0.97	0.95	0.97	0.99	0.97	0.96	0.96	0.98	0.98	0.99	0.98	0.99	0.95	0.98
642.16		1.02	0.98	0.96	1.01	0.97	0.99	0.93	0.98	0.99	0.96	0.98	0.97	0.95	0.96	0.99	0.97	0.96	0.96	0.98	0.98	0.99	0.98	0.99	0.94	0.98
642.93		1.02	0.98	0.96	1.01	0.98	0.99	0.93	0.98	0.99	0.96	0.98	0.97	0.95	0.97	0.99	0.97	0.96	0.96	0.98	0.98	0.99	0.98	0.99	0.95	0.98
643.70		1.02	0.98	0.96	1.01	0.98	0.99	0.93	0.98	0.99	0.96	0.98	0.97	0.95	0.96	0.99	0.97	0.96	0.96	0.97	0.98	0.99	0.98	0.99	0.95	0.98
644.47		1.02	0.98	0.96	1.01	0.98	0.99	0.93	0.98	0.99	0.96	0.98	0.97	0.95	0.96	1.00	0.97	0.96	0.96	0.98	0.98	0.99	0.98	0.99	0.95	0.98
645.25		1.02	0.98	0.96	1.01	0.97	0.99	0.93	0.99	0.99	0.96	0.98	0.97	0.96	0.96	0.99	0.98	0.96	0.96	0.98	0.98	0.99	0.98	0.99	0.95	0.98
646.02		1.01	0.98	0.96	1.01	0.98	0.99	0.93	0.99	0.99	0.96	0.98	0.97	0.95	0.97	0.99	0.97	0.96	0.96	0.98	0.98	0.99	0.98	0.99	0.95	0.98
646.79		1.02	0.98	0.96	1.01	0.98	0.99	0.93	0.98	0.99	0.96	0.98	0.97	0.96	0.97	0.99	0.98	0.96	0.96	0.98	0.98	0.99	0.98	0.99	0.95	0.98
647.57		1.02	0.98	0.96	1.01	0.98	0.99	0.93	0.98	1.00	0.96	0.98	0.97	0.96	0.97	0.99	0.97	0.96	0.96	0.97	0.98	0.99	0.98	0.99	0.95	0.98
648.34		1.02	0.98	0.96	1.01	0.98	0.99	0.93	0.97	1.00	0.96	0.98	0.97	0.96	0.97	0.99	0.97	0.97	0.96	0.98	0.98	0.99	0.98	0.99	0.95	0.98
649.11		1.02	0.98	0.96	1.01	0.98	0.99	0.93	0.97	1.00	0.96	0.98	0.97	0.96	0.97	0.99	0.97	0.96	0.96	0.98	0.98	0.99	0.98	0.99	0.95	0.98
649.88		1.02	0.98	0.96	1.01	0.98	0.99	0.93	0.97	1.00	0.96	0.98	0.97	0.96	0.97	0.99	0.97	0.97	0.96	0.98	0.98	0.99	0.98	1.00	0.95	0.98
650.66		1.02	0.98	0.96	1.01	0.97	0.99	0.93	0.97	1.00	0.96	0.98	0.97	0.96	0.97	0.99	0.97	0.96	0.96	0.98	0.98	0.99	0.98	1.00	0.95	0.98
651.43		1.01	0.98	0.95	1.03	0.97	0.99	0.93	0.95	1.00	0.95	0.99	0.97	0.96	0.97	0.99	0.97	0.97	0.96	0.98	0.95	1.00	0.98	1.00	0.95	0.97
652.20		1.01	0.97	1.01	1.02	0.99	0.99	0.93	0.97	1.01	0.95	0.99	0.97	0.96	0.97	0.99	0.97	0.96	1.03	0.98	0.95	0.99	0.99	1.01	0.95	1.00
652.97		1.01	0.97	1.03	1.02	1.00	0.99	0.93	0.98	1.01	0.99	0.99	0.97	0.96	0.97	0.99	0.97	0.96	1.05	0.98	0.95	0.98	0.99	1.01	0.95	1.00
653.75		1.00	0.96	1.04	1.02	1.00	0.99	0.95	0.98	1.01	1.01	0.99	0.97	0.96	0.96	0.99	0.97	0.97	1.06	0.98	0.95	0.98	0.99	1.01	0.95	1.01
654.52		1.00	0.96	1.05	1.02	1.00	0.99	0.95	0.99	1.01	1.02	0.99	0.97	0.96	0.97	0.99	0.97	0.97	1.07	0.98	0.95	0.98	0.99	1.01	0.95	1.01
655.29		1.00	0.96	1.05	1.02	1.01	0.99	0.95	0.99	1.01	1.03	0.99	0.98	0.98	0.98	0.99	0.99	0.97	1.07	0.99	0.95	0.98	0.99	1.01	0.95	1.01
656.06		1.00	0.96	1.06	1.02	1.01	1.00	0.95	0.99	1.01	0.98	0.99	0.98	0.98	0.97	0.99	0.99	0.97	1.08	0.98	0.95	0.98	0.99	1.01	0.96	1.01

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
656.83		1.00	0.97	1.01	1.01	1.00	0.99	0.93	0.95	1.01	0.95	0.99	0.97	0.96	0.96	0.99	0.97	0.97	1.00	0.97	0.96	0.99	0.99	0.99	0.95	0.97
657.61		1.00	0.97	0.99	1.00	1.00	0.99	0.90	0.94	1.01	0.95	0.98	0.97	0.93	0.95	0.99	0.94	0.97	0.96	0.96	0.96	0.99	0.99	0.99	0.95	0.94
658.38		1.00	0.97	0.98	1.00	0.99	0.99	0.93	0.93	1.01	0.93	0.98	0.95	0.93	0.94	0.99	0.93	0.97	0.94	0.95	0.97	0.99	0.99	0.98	0.95	0.93
659.15		1.00	0.98	0.95	1.00	0.99	0.99	0.93	0.91	1.01	0.90	0.98	0.97	0.96	0.97	0.99	0.98	0.97	0.90	0.98	0.97	1.00	0.99	0.98	0.95	0.91
659.92		1.00	0.99	0.91	0.99	0.98	0.99	0.94	0.89	1.01	0.84	0.98	0.97	0.96	0.97	0.99	0.97	0.97	0.85	0.98	0.98	1.01	0.99	0.97	0.96	0.88
660.69		1.01	1.00	0.83	0.98	0.96	0.98	0.94	0.85	1.01	0.71	0.97	0.97	0.97	0.97	1.00	0.97	0.97	0.76	0.98	1.00	1.04	0.99	0.94	0.96	0.82
661.46		1.01	1.08	0.55	0.93	0.88	0.96	0.94	0.73	0.99	0.63	0.93	0.97	0.96	0.97	1.01	0.98	0.97	0.55	0.98	1.09	1.15	0.98	0.87	0.96	0.69
662.24		1.01	0.98	0.96	1.01	0.98	0.99	0.94	0.91	1.00	0.97	0.99	0.98	0.96	0.97	0.99	0.97	0.97	0.69	0.98	0.99	0.99	0.98	1.00	0.95	0.75
663.01		1.01	0.98	0.96	1.01	0.98	0.99	0.94	0.98	1.01	0.97	0.99	0.97	0.96	0.97	0.99	0.98	0.97	0.96	0.98	0.98	0.99	0.98	1.00	0.96	0.99
663.78		1.01	0.99	0.96	1.01	0.98	0.99	0.94	0.98	1.01	0.97	0.99	0.97	0.96	0.97	0.99	0.97	0.97	0.96	0.98	0.98	0.99	0.98	1.00	0.96	0.99
664.55		1.01	0.98	0.96	1.01	0.98	0.99	0.94	0.98	1.01	0.97	0.99	0.97	0.96	0.97	0.99	0.97	0.97	0.96	0.98	0.98	0.99	0.99	1.00	0.95	0.99
665.32		1.01	0.98	0.97	1.01	0.98	0.99	0.94	0.98	1.01	0.97	0.99	0.98	0.96	0.97	0.99	0.98	0.97	0.97	0.99	0.98	0.99	0.98	1.00	0.96	0.99
666.09		1.01	0.98	0.97	1.01	0.98	0.99	0.94	0.98	1.01	0.97	0.99	0.98	0.96	0.97	0.99	0.97	0.97	0.96	0.98	0.98	0.99	0.98	0.99	0.96	0.99
666.86		1.01	0.98	0.97	1.01	0.98	0.99	0.94	0.99	1.00	0.97	0.99	0.98	0.97	0.97	0.99	0.98	0.97	0.97	0.98	0.98	0.99	0.99	0.99	0.96	0.99
667.63		1.01	0.98	0.97	1.01	0.98	0.99	0.94	0.98	1.00	0.97	0.99	0.98	0.97	0.97	0.99	0.98	0.97	0.96	0.98	0.98	0.99	0.98	1.00	0.96	1.01
668.40		1.01	0.99	0.97	1.01	0.98	0.99	0.94	0.98	1.00	0.97	0.99	0.98	0.96	0.98	0.99	0.97	0.97	0.96	0.98	0.98	0.99	0.98	1.00	0.96	1.00
669.18		1.01	0.98	0.97	1.01	0.98	0.99	0.94	0.97	1.00	0.96	0.99	0.98	0.96	0.98	0.99	0.98	0.97	0.96	0.98	0.98	0.99	0.98	1.00	0.96	1.00
669.95		1.01	0.99	0.97	1.01	0.98	0.99	0.94	0.97	1.00	0.96	0.99	0.98	0.96	0.97	0.99	0.98	0.97	0.97	0.98	0.98	0.99	0.98	1.00	0.96	1.00
670.72		1.01	0.99	0.96	1.01	0.98	0.99	0.94	0.97	1.00	0.96	0.99	0.98	0.96	0.97	0.99	0.97	0.97	0.96	0.98	0.98	1.00	0.98	1.00	0.96	1.00
671.49		1.02	0.99	0.96	1.01	0.98	0.99	0.94	0.97	1.00	0.96	0.99	0.97	0.96	0.97	0.99	0.97	0.97	0.97	0.99	0.98	1.00	0.98	1.00	0.96	0.99
672.26		1.02	0.99	0.96	1.01	0.98	0.99	0.94	0.97	1.00	0.96	0.99	0.98	0.97	0.98	0.99	0.97	0.98	0.97	0.98	0.98	1.00	0.98	1.00	0.96	0.99
673.03		1.02	0.99	0.96	1.01	0.98	0.99	0.94	0.97	1.00	0.96	0.99	0.98	0.97	0.98	0.99	0.98	0.97	0.97	0.98	0.99	0.99	0.98	1.00	0.95	0.98
673.80		1.02	0.98	0.96	1.01	0.98	0.99	0.94	0.97	1.00	0.96	0.99	0.98	0.97	0.97	0.99	0.98	0.98	0.97	0.98	0.99	0.99	0.99	1.00	0.96	0.99
674.57		1.02	0.99	0.97	1.01	0.98	0.99	0.94	0.98	1.01	0.97	0.99	0.98	0.97	0.98	0.99	0.98	0.98	0.97	0.98	0.99	0.99	0.98	1.00	0.96	0.98

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
675.34		1.01	0.99	0.97	1.01	0.98	0.99	0.94	0.98	1.01	0.97	0.99	0.98	0.97	0.98	0.99	0.98	0.98	0.97	0.98	0.99	0.99	0.98	1.00	0.96	0.98
676.11		1.01	0.99	0.97	1.01	0.98	0.99	0.94	0.98	1.01	0.97	0.99	0.98	0.97	0.98	0.99	0.98	0.98	0.97	0.98	0.99	0.99	0.99	1.00	0.96	0.98
676.88		1.01	0.98	0.98	1.01	0.98	0.99	0.95	0.98	1.01	0.97	0.99	0.98	0.97	0.98	0.99	0.98	0.98	0.97	0.98	0.99	0.99	0.99	1.00	0.97	0.98
677.65		1.01	0.98	0.97	1.01	0.98	0.99	0.94	0.98	1.01	0.97	0.99	0.98	0.97	0.97	0.99	0.98	0.98	0.97	0.98	0.98	0.99	0.98	1.00	0.96	0.98
678.42		1.01	0.99	0.98	1.01	0.98	0.99	0.95	0.98	1.01	0.97	0.99	0.98	0.97	0.97	1.00	0.98	0.98	0.97	0.98	0.98	0.99	0.98	1.00	0.96	0.98
679.19		1.01	0.99	0.98	1.01	0.98	0.99	0.94	0.98	1.01	0.97	0.99	0.98	0.97	0.98	1.00	0.98	0.98	0.97	0.98	0.99	0.99	0.98	1.00	0.96	0.98
679.96		1.01	0.98	0.97	1.01	0.98	0.99	0.94	0.98	1.01	0.97	0.99	0.98	0.97	0.97	1.00	0.98	0.98	0.97	0.98	0.99	1.00	0.98	1.00	0.96	0.98
680.73		1.02	0.98	0.97	1.01	0.98	0.99	0.95	0.97	1.00	0.97	0.99	0.98	0.97	0.98	1.01	0.98	0.98	0.97	0.99	0.99	1.00	0.98	0.99	0.97	0.98
681.50		1.01	0.98	0.97	1.01	0.98	0.99	0.95	0.98	1.00	0.97	0.99	0.98	0.97	0.97	1.00	0.98	0.98	0.97	0.98	0.99	1.00	0.98	1.00	0.96	0.98
682.27		1.01	0.98	0.97	1.01	0.98	0.99	0.95	0.97	1.00	0.97	0.99	0.98	0.97	0.98	1.00	0.98	0.98	0.97	0.99	0.99	1.00	0.99	0.99	0.96	0.98
683.04		1.01	0.98	0.97	1.01	0.99	0.99	0.95	0.97	1.00	0.97	0.99	0.98	0.97	0.98	1.00	0.98	0.98	0.97	0.98	0.99	1.00	0.99	1.00	0.96	0.98
683.81		1.01	0.98	0.97	1.01	0.99	0.99	0.95	0.97	1.00	0.96	0.99	0.98	0.97	0.97	1.00	0.98	0.98	0.97	0.98	0.99	0.99	0.99	1.00	0.97	0.98
684.58		1.01	0.98	0.97	1.01	0.99	0.99	0.94	0.97	1.01	0.96	0.99	0.98	0.97	0.98	1.00	0.98	0.98	0.97	0.99	0.99	0.99	0.99	1.00	0.96	0.98
685.35		1.01	0.98	0.97	1.01	0.99	0.99	0.95	0.97	1.01	0.96	0.99	0.98	0.97	0.98	1.01	0.98	0.98	0.97	0.99	0.99	0.99	0.99	1.00	0.97	0.98
686.11		1.01	0.98	0.97	1.01	0.99	0.99	0.95	0.97	1.00	0.97	0.99	0.98	0.97	0.98	1.00	0.98	0.98	0.97	0.98	0.99	0.99	0.99	1.00	0.96	0.98
686.88		1.01	0.98	0.97	1.01	0.99	0.99	0.95	0.97	1.00	0.96	0.99	0.98	0.97	0.98	1.00	0.98	0.98	0.97	0.98	0.99	0.99	0.99	1.00	0.96	0.98
687.65		1.01	0.98	0.97	1.01	0.99	0.99	0.95	0.97	1.00	0.97	0.99	0.98	0.97	0.98	1.00	0.98	0.98	0.97	0.98	0.99	0.99	0.99	1.00	0.97	0.98
688.42		1.01	0.98	0.97	1.01	0.99	0.99	0.95	0.97	1.00	0.97	0.99	0.98	0.98	0.98	1.00	0.98	0.98	0.98	0.99	0.99	0.99	0.99	1.00	0.97	0.98
689.19		1.01	0.98	0.97	1.01	0.99	0.99	0.95	0.97	1.00	0.97	0.99	0.98	0.97	0.98	0.99	0.98	0.98	0.97	0.99	0.99	0.99	0.99	1.00	0.97	0.99
689.96		1.01	0.99	0.97	1.01	0.99	0.99	0.95	0.97	1.00	0.97	0.99	0.99	0.97	0.98	0.99	0.98	0.98	0.97	0.98	0.99	1.00	0.99	0.99	0.96	0.99
690.73		1.01	0.98	0.97	1.01	0.99	1.00	0.95	0.97	1.00	0.97	0.99	0.98	0.97	0.98	0.99	0.98	0.98	0.98	0.99	0.99	1.00	0.99	0.99	0.97	0.99
691.50		1.01	0.99	0.97	1.01	0.99	1.00	0.95	0.97	1.00	0.97	0.99	0.98	0.98	0.98	0.99	0.98	0.98	0.98	0.99	0.99	1.00	0.99	0.99	0.97	0.99
692.27		1.01	0.99	0.97	1.01	0.99	1.00	0.95	0.97	1.00	0.97	0.99	0.98	0.98	0.98	0.99	0.98	0.98	0.97	0.99	0.99	1.00	0.99	0.99	0.97	0.99
693.03		1.01	0.99	0.97	1.01	0.99	1.00	0.95	0.97	1.00	0.97	0.99	0.99	0.97	0.98	0.99	0.98	0.98	0.97	0.98	0.99	1.00	0.99	1.00	0.97	0.99

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
693.80		1.01	0.99	0.97	1.01	0.99	1.00	0.95	0.97	1.00	0.97	0.99	0.98	0.97	0.98	0.99	0.98	0.98	0.97	0.98	0.99	1.00	0.99	1.00	0.97	0.99
694.57		1.01	0.98	0.97	1.01	0.99	1.00	0.95	0.97	1.00	0.97	0.99	0.98	0.98	0.98	0.99	0.98	0.99	0.97	0.99	0.99	1.00	0.98	1.00	0.97	0.99
695.34		1.01	0.98	0.98	1.01	0.99	1.00	0.95	0.97	1.00	0.97	0.99	0.98	0.98	0.98	0.99	0.98	0.99	0.97	0.99	0.99	1.00	0.99	1.00	0.97	0.99
696.11		1.01	0.98	0.98	1.01	0.99	1.00	0.95	0.97	1.01	0.97	0.99	0.98	0.98	0.98	0.99	0.98	0.98	0.97	0.99	0.99	1.00	0.99	1.00	0.97	0.99
696.88		1.01	0.98	0.98	1.01	0.99	1.00	0.95	0.96	1.01	0.97	0.99	0.98	0.97	0.98	0.99	0.98	0.98	0.97	0.98	0.99	1.00	0.99	1.00	0.97	0.99
697.64		1.01	0.98	0.98	1.01	0.99	1.00	0.95	0.96	1.01	0.97	0.99	0.98	0.97	0.98	0.99	0.98	0.98	0.97	0.99	0.99	1.00	0.99	1.00	0.97	0.99
698.41		1.01	0.98	0.98	1.01	0.99	1.00	0.95	0.97	1.00	0.97	0.99	0.98	0.98	0.98	0.99	0.98	0.99	0.97	0.99	0.99	0.99	0.99	1.00	0.97	0.99
699.18		1.01	0.98	0.98	1.02	0.99	0.99	0.95	0.97	1.00	0.97	0.99	0.98	0.97	0.98	0.99	0.98	0.99	0.97	0.99	0.99	0.99	0.99	0.99	0.97	0.98
699.95		1.01	0.99	0.97	1.01	0.99	0.99	0.95	0.97	1.00	0.97	0.99	0.98	0.98	0.98	0.99	0.98	0.99	0.97	0.99	0.99	0.99	0.99	0.99	0.97	0.98
700.72		1.01	0.98	0.97	1.01	0.99	1.00	0.95	0.97	1.00	0.97	0.99	0.98	0.98	0.98	0.99	0.99	0.98	0.97	0.99	0.99	0.99	0.99	0.99	0.97	0.98
701.48		1.01	0.99	0.97	1.01	0.99	1.00	0.96	0.97	0.99	0.97	0.99	0.99	0.98	0.98	0.99	0.98	0.98	0.97	0.99	0.99	0.99	0.99	0.99	0.97	0.99
702.25		1.01	0.99	0.97	1.01	0.99	1.00	0.96	0.97	1.00	0.97	0.99	0.99	0.97	0.98	0.99	0.99	0.99	0.98	0.99	0.99	0.99	0.99	0.99	0.97	0.99
703.02		1.01	0.99	0.97	1.01	0.99	1.00	0.96	0.97	1.00	0.97	0.99	0.98	0.98	0.98	0.99	0.98	0.98	0.98	0.99	0.99	0.99	0.99	0.99	0.97	0.99
703.79		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.97	1.00	0.97	0.99	0.99	0.98	0.98	1.00	0.98	0.99	0.98	0.99	0.99	0.99	0.99	0.99	0.97	0.99
704.55		1.01	0.99	0.98	1.01	0.99	0.99	0.96	0.97	1.00	0.97	0.99	0.98	0.98	0.98	1.00	0.98	0.99	0.97	0.99	0.99	0.99	0.99	1.00	0.97	0.99
705.32		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.97	1.01	0.97	0.99	0.98	0.98	0.98	1.00	0.98	0.99	0.97	0.99	0.99	0.99	0.99	1.00	0.98	0.99
706.09		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.97	1.01	0.97	0.99	0.98	0.98	0.98	1.00	0.99	0.99	0.98	0.99	0.99	0.99	0.99	1.00	0.98	0.99
706.86		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.96	1.01	0.97	0.99	0.99	0.98	0.98	1.00	0.98	0.99	0.97	0.99	0.99	0.99	0.99	1.00	0.97	0.99
707.62		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.96	1.01	0.97	0.99	0.98	0.98	0.98	1.00	0.99	0.99	0.97	0.99	0.99	0.99	0.99	1.00	0.98	0.99
708.39		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.97	1.01	0.97	0.99	0.98	0.98	0.98	1.00	0.99	0.99	0.97	0.99	0.99	0.99	0.99	1.00	0.97	0.99
709.16		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.97	1.01	0.98	0.99	0.99	0.98	0.98	1.00	0.99	0.99	0.98	0.99	0.99	0.99	0.99	1.00	0.97	0.99
709.92		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.97	1.01	0.98	0.99	0.99	0.98	0.98	1.00	0.99	0.99	0.98	0.99	0.99	0.99	0.99	1.00	0.98	0.99
710.69		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.97	1.02	0.98	0.99	0.98	0.98	0.98	1.00	0.99	0.99	0.98	0.99	0.99	0.99	0.99	1.00	0.97	0.99
711.46		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.97	1.02	0.98	0.99	0.99	0.98	0.98	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
712.23		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.97	1.02	0.98	0.99	0.98	0.98	0.98	1.00	0.98	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
712.99		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.97	1.01	0.98	0.99	0.99	0.98	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.97	0.98
713.76		1.01	0.99	0.98	1.02	0.99	1.00	0.96	0.97	1.01	0.98	0.99	0.99	0.98	0.98	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
714.53		1.01	0.99	0.98	1.02	0.99	1.00	0.96	0.97	1.01	0.98	0.99	0.98	0.98	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
715.29		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.98	1.01	0.98	0.99	0.98	0.98	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.97	0.98
716.06		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.98	1.01	0.98	1.00	0.99	0.98	0.99	1.00	0.98	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
716.82		1.01	0.99	0.98	1.01	0.99	1.00	0.96	0.98	1.00	0.98	1.00	0.99	0.98	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
717.59		1.01	0.99	0.98	1.01	0.99	1.00	0.97	0.98	1.00	0.98	1.00	0.98	0.98	0.99	1.00	0.99	0.99	0.98	0.99	1.00	1.00	0.99	1.00	0.98	0.99
718.36		1.01	0.99	0.98	1.02	0.99	1.00	0.97	0.98	1.00	0.98	1.00	0.99	0.98	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
719.12		1.01	0.99	0.98	1.01	0.99	1.00	0.97	0.98	1.00	0.98	1.00	0.99	0.98	0.99	1.00	0.99	0.99	0.98	0.99	1.00	1.00	0.99	1.00	0.98	0.99
719.89		1.01	0.99	0.98	1.01	0.99	1.00	0.97	0.99	1.00	0.98	1.00	0.99	0.98	0.98	1.00	0.98	0.99	0.98	0.99	1.00	1.00	0.99	1.00	0.98	0.99
720.65		1.01	0.99	0.98	1.02	0.99	1.00	0.97	0.99	1.00	0.98	1.00	0.99	0.98	0.99	1.00	0.98	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
721.42		1.01	0.99	0.98	1.02	0.99	1.00	0.97	0.99	1.00	0.98	1.00	0.99	0.98	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
722.19		1.01	0.99	0.98	1.02	0.99	1.00	0.97	0.99	1.01	0.98	1.00	0.99	0.98	0.99	1.00	0.98	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
722.95		1.02	0.99	0.98	1.02	0.99	1.00	0.97	0.99	1.01	0.98	0.99	0.99	0.98	0.99	0.99	0.98	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
723.72		1.02	0.99	0.98	1.02	0.99	1.00	0.97	0.99	1.01	0.98	1.00	0.99	0.98	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
724.48		1.02	0.99	0.99	1.02	0.99	1.00	0.97	0.99	1.01	0.98	1.00	0.99	0.98	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
725.25		1.02	0.99	0.98	1.02	0.99	1.00	0.97	0.99	1.01	0.98	1.00	0.99	0.98	0.98	1.00	0.98	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
726.01		1.01	0.99	0.98	1.01	0.99	1.00	0.97	0.99	1.01	0.99	1.00	0.99	0.98	0.98	0.99	0.98	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
726.78		1.01	0.99	0.98	1.01	0.99	1.00	0.97	0.99	1.01	0.98	0.99	0.99	0.98	0.98	1.00	0.98	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
727.55		1.01	0.99	0.98	1.01	0.99	1.00	0.97	0.98	1.01	0.98	0.99	0.99	0.98	0.99	0.99	0.98	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.99	0.99
728.31		1.01	0.99	0.98	1.01	0.99	1.00	0.97	0.98	1.01	0.98	0.99	0.99	0.99	0.99	1.00	0.98	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
729.08		1.01	0.99	0.98	1.01	0.99	1.00	0.97	0.98	1.01	0.98	0.99	0.99	0.98	0.99	1.00	0.98	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
729.84		1.01	0.99	0.98	1.01	0.99	1.00	0.97	0.97	1.01	0.98	0.99	0.99	0.98	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
730.61		1.00	0.99	0.98	1.02	0.99	1.00	0.97	0.97	1.01	0.98	0.99	0.99	0.98	0.98	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
731.37		1.00	0.99	0.98	1.02	0.99	1.00	0.97	0.97	1.01	0.97	0.99	0.99	0.98	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.99	0.98
732.14		1.00	0.99	0.98	1.02	0.99	1.00	0.98	0.97	1.01	0.97	0.99	0.99	0.98	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
732.90		1.00	0.99	0.98	1.02	0.99	1.00	0.98	0.97	1.00	0.97	0.99	0.99	0.98	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
733.67		1.00	0.99	0.98	1.02	0.99	1.00	0.97	0.97	1.00	0.97	0.99	0.99	0.98	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
734.43		1.00	0.99	0.98	1.02	0.99	1.00	0.98	0.97	1.00	0.96	0.99	0.99	0.98	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
735.20		1.00	0.99	0.98	1.02	0.99	1.00	0.97	0.97	1.00	0.96	0.99	0.99	0.98	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
735.96		1.01	0.99	0.99	1.01	0.99	1.00	0.98	0.97	1.00	0.96	0.99	0.99	0.98	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
736.72		1.01	0.99	0.99	1.01	0.99	1.00	0.98	0.97	1.00	0.97	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.98
737.49		1.00	0.99	0.99	1.01	0.99	1.00	0.98	0.97	1.00	0.97	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
738.25		1.01	0.99	0.99	1.01	0.99	1.00	0.98	0.98	1.00	0.97	0.99	0.99	0.98	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
739.02		1.01	0.99	0.99	1.01	0.99	1.00	0.98	0.98	1.00	0.97	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.98	0.99	1.00	1.00	0.99	1.00	0.98	0.99
739.78		1.01	0.99	0.99	1.01	0.99	1.00	0.98	0.98	1.00	0.97	0.99	0.99	0.98	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.98	0.99
740.55		1.01	0.99	0.99	1.01	0.99	1.00	0.98	0.98	1.00	0.97	1.00	0.99	0.99	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.99	0.99
741.31		1.01	0.99	0.99	1.01	0.99	0.99	0.98	0.98	1.00	0.98	1.00	0.99	0.98	0.99	1.00	0.99	0.99	0.98	0.99	0.99	0.99	0.99	1.00	0.99	0.99
742.07		1.01	0.99	0.99	1.01	0.99	1.00	0.98	0.99	1.00	0.97	1.00	0.99	0.99	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.99	0.99
742.84		1.01	0.99	0.98	1.01	0.99	1.00	0.98	0.99	1.00	0.98	1.00	0.99	0.98	0.99	1.00	0.99	0.99	0.98	1.00	0.99	1.00	0.99	1.00	0.99	0.99
743.60		1.01	0.99	0.98	1.02	0.99	1.00	0.98	0.99	1.00	0.98	1.00	0.99	0.98	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.99	0.99
744.36		1.01	0.99	0.98	1.02	0.99	1.00	0.98	0.99	1.00	0.98	0.99	0.99	0.99	0.99	1.00	0.99	0.99	0.98	1.00	0.99	1.00	0.99	1.00	0.99	0.99
745.13		1.01	0.99	0.98	1.02	0.99	0.99	0.98	0.99	1.00	0.99	0.99	0.99	0.99	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.99	0.99
745.89		1.00	0.99	0.98	1.02	0.99	0.99	0.98	1.00	0.99	0.98	0.99	0.99	0.99	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	0.99	0.99	0.99
746.66		1.00	0.99	0.98	1.02	0.99	1.00	0.98	1.00	0.99	0.98	0.99	0.99	0.99	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	0.99	0.99	0.99
747.42		1.00	0.99	0.98	1.02	0.99	1.00	0.98	1.00	0.99	0.98	0.99	1.00	0.99	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	0.99	0.99	0.99
748.18		1.00	0.99	0.98	1.02	0.99	1.00	0.98	0.99	0.99	0.98	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	0.99	0.98	0.99

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
748.95		1.00	0.99	0.99	1.02	0.99	1.00	0.98	0.99	0.99	0.98	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	0.99	0.99	0.98
749.71		1.00	0.99	0.99	1.02	0.99	1.00	0.98	0.99	0.99	0.98	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	0.99	0.99	0.99	0.99
750.47		1.00	0.99	0.99	1.02	0.99	1.00	0.98	0.99	0.99	0.98	1.00	0.99	0.99	0.99	0.99	1.00	0.99	0.98	1.00	1.00	1.00	0.99	1.00	0.99	0.99
751.24		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.98	0.99	0.98	1.00	0.99	0.99	0.99	0.99	0.99	0.99	0.98	0.99	1.00	1.00	0.99	0.99	0.99	0.98
752.00		1.00	0.99	0.99	1.01	0.99	1.00	0.98	0.98	0.99	0.98	1.00	0.99	0.99	0.99	0.99	0.99	0.99	0.98	0.99	0.99	1.00	1.00	0.99	0.99	0.98
752.76		1.00	0.99	0.99	1.02	0.99	1.00	0.98	0.98	0.99	0.98	1.00	0.99	0.99	0.99	1.00	0.99	0.99	0.98	1.00	0.99	1.00	1.00	0.99	0.99	0.98
753.52		1.00	0.99	0.98	1.02	0.99	1.00	0.99	0.98	0.99	0.98	1.00	0.99	0.99	0.99	0.99	0.99	0.99	0.98	1.00	0.99	1.00	0.99	0.99	0.99	0.98
754.29		1.00	0.99	0.98	1.02	0.99	1.00	0.99	0.98	1.00	0.97	1.00	1.00	0.99	0.99	1.00	0.99	0.99	0.98	1.00	0.99	1.00	1.00	0.99	0.99	0.98
755.05		1.00	0.99	0.98	1.02	0.99	1.00	0.98	0.97	1.00	0.97	1.00	0.99	0.99	0.99	1.00	1.00	0.99	0.98	0.99	0.99	1.00	0.99	0.99	0.99	0.98
755.81		1.00	0.99	0.98	1.02	0.99	1.00	0.99	0.97	1.00	0.97	1.00	0.99	0.99	0.99	1.00	1.00	0.99	0.98	0.99	0.99	1.00	0.99	0.99	0.99	0.98
756.58		1.00	0.99	0.98	1.02	0.99	1.00	0.99	0.97	1.00	0.97	1.00	1.00	0.99	0.99	1.00	1.00	0.99	0.98	1.00	0.99	1.00	0.99	1.00	0.99	0.98
757.34		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.96	1.00	0.97	1.00	1.00	0.99	0.99	1.00	1.00	0.99	0.98	1.00	0.99	1.00	0.99	1.00	0.99	0.98
758.10		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.97	1.00	0.97	0.99	1.00	0.99	0.99	1.00	0.99	0.99	0.98	0.99	0.99	1.00	0.99	1.00	0.99	0.98
758.86		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.97	1.00	0.97	0.99	1.00	0.99	0.99	1.00	1.00	0.99	0.98	1.00	0.99	1.00	0.99	1.00	0.99	0.98
759.63		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.97	1.00	0.97	0.99	0.99	0.99	0.99	1.00	0.99	0.99	0.98	1.00	0.99	1.00	0.99	1.00	0.99	0.98
760.39		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.97	1.00	0.97	0.99	0.99	0.99	0.99	1.00	1.00	0.99	0.98	1.00	0.99	1.00	0.99	1.00	0.99	0.98
761.15		1.00	0.99	0.99	1.02	1.00	1.00	0.99	0.97	1.00	0.97	0.99	1.00	0.99	0.99	0.99	1.00	0.99	0.98	1.00	0.99	1.00	0.99	1.00	0.99	0.98
761.91		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.97	1.00	0.97	0.99	0.99	0.99	0.99	1.00	0.99	0.99	0.98	1.00	0.99	1.00	0.99	0.99	0.99	0.98
762.67		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.97	1.00	0.97	0.99	0.99	0.99	0.99	1.00	1.00	0.99	0.98	1.00	0.99	1.00	0.99	0.99	0.99	0.98
763.44		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.97	1.00	0.97	0.99	0.99	0.99	0.99	1.00	1.00	0.99	0.98	0.99	1.00	1.00	0.99	0.99	0.99	0.98
764.20		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.97	1.00	0.98	0.99	1.00	0.99	1.00	0.99	1.00	0.99	0.98	1.00	1.00	1.00	0.99	0.99	1.00	0.98
764.96		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.97	1.00	0.98	1.00	0.99	0.99	1.00	0.99	0.99	0.99	0.98	1.00	1.00	1.00	0.99	1.00	0.99	0.99
765.72		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.97	1.00	0.98	0.99	1.00	1.00	1.00	1.00	1.00	0.99	0.98	1.00	1.00	1.00	0.99	1.00	0.99	0.98
766.48		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.97	1.00	0.98	0.99	0.99	0.99	0.99	1.00	1.00	0.99	0.98	1.00	1.00	1.00	0.99	1.00	1.00	0.99

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
767.24		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.98	1.00	0.98	0.99	1.00	0.99	0.99	0.99	1.00	0.99	0.98	1.00	1.00	1.00	0.99	1.00	0.99	0.99
768.01		1.00	0.99	0.99	1.02	1.00	1.00	0.99	0.98	0.99	0.98	0.99	1.00	0.99	0.99	0.99	1.00	0.99	0.98	1.00	1.00	1.00	0.99	1.00	0.99	0.99
768.77		1.00	0.99	0.99	1.02	0.99	1.00	0.99	0.98	0.99	0.98	0.99	1.00	0.99	0.99	0.99	1.00	1.00	0.98	1.00	1.00	1.00	0.99	1.00	0.99	0.99
769.53		1.00	0.99	0.99	1.02	1.00	1.00	0.99	0.98	0.99	0.98	0.99	0.99	1.00	1.00	1.00	1.00	0.99	0.98	1.00	1.00	1.00	0.99	1.00	0.99	0.99
770.29		1.00	0.99	0.99	1.02	1.00	1.00	0.99	0.98	0.99	0.98	0.99	1.00	0.99	0.99	1.00	1.00	0.99	0.98	1.00	1.00	1.00	0.99	1.00	1.00	0.99
771.05		1.00	0.99	0.98	1.01	1.00	1.00	0.99	0.98	0.99	0.98	1.00	1.00	0.99	1.00	0.99	1.00	0.99	0.98	0.99	1.00	1.00	0.99	1.00	0.99	0.99
771.81		1.00	0.99	0.99	1.01	1.00	1.00	0.99	0.99	0.99	0.98	0.99	1.00	0.99	0.99	0.99	1.00	1.00	0.98	1.00	1.00	1.00	0.99	0.99	1.00	0.99
772.57		1.00	0.99	0.99	1.01	1.00	1.00	0.99	0.99	0.99	0.98	0.99	1.00	1.00	0.99	0.99	1.00	1.00	0.98	1.00	1.00	1.00	0.99	0.99	1.00	0.98
773.33		1.00	0.99	0.99	1.02	1.00	1.00	0.99	0.99	0.99	0.99	0.99	1.00	0.99	1.00	0.99	1.00	1.00	0.98	1.00	1.00	1.00	0.99	0.99	0.99	0.98
774.10		1.00	0.99	0.99	1.02	1.00	1.00	0.99	0.99	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	0.99	0.99	1.00	0.98
774.86		1.00	0.99	0.99	1.02	1.00	1.00	0.99	1.00	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	0.99	0.99	1.00	0.99
775.62		1.00	0.99	0.99	1.02	1.00	1.00	0.99	0.99	0.99	0.99	1.00	1.00	0.99	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	0.99	0.99	1.00	0.99
776.38		1.00	0.99	0.99	1.02	1.00	1.00	0.99	0.99	0.99	0.99	0.99	1.00	0.99	1.00	1.00	1.00	0.99	0.99	1.00	1.00	1.00	0.99	0.99	0.99	0.99
777.14		1.00	0.99	0.99	1.02	1.00	1.00	0.99	0.99	0.99	0.99	0.99	1.00	1.00	1.00	0.99	1.00	1.00	0.99	1.00	1.00	1.00	0.99	1.00	1.00	0.99
777.90		1.00	0.99	0.99	1.02	1.00	1.00	0.99	0.99	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	0.99	1.00	0.99	1.00	1.00	0.99
778.66		1.00	0.99	0.99	1.02	1.00	1.00	1.00	0.99	0.99	0.98	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	0.99	1.00	0.99	1.00	1.00	0.99
779.42		1.00	0.99	0.99	1.02	1.00	1.00	1.00	0.98	0.99	0.98	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	0.99	1.00	0.99	1.00	1.00	0.99
780.18		1.00	0.99	0.99	1.02	1.00	1.01	0.99	0.98	0.99	0.98	0.99	1.00	1.00	0.99	1.00	1.00	1.00	0.99	1.00	1.00	1.00	0.99	1.00	0.99	0.99
780.94		1.00	0.99	0.99	1.02	1.00	1.01	1.00	0.98	0.99	0.98	0.99	1.00	1.00	1.00	0.99	1.00	1.00	0.99	1.00	1.00	1.00	0.99	1.00	1.00	0.99
781.70		1.00	0.99	0.99	1.02	1.00	1.01	1.00	0.98	0.99	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	0.99	1.00	1.00	0.99
782.46		1.00	0.99	0.99	1.02	1.00	1.01	0.99	0.98	0.99	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99
783.22		1.00	0.99	0.99	1.02	1.00	1.01	0.99	0.98	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99
783.98		1.00	0.99	0.99	1.02	1.00	1.01	1.00	0.98	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99
784.74		1.00	0.99	0.99	1.02	1.00	1.00	1.00	0.99	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99

	Bat ID*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
785.50		1.00	0.99	0.99	1.02	1.00	1.00	1.00	0.99	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	0.99	1.00	1.00	0.99
786.26		1.00	0.99	0.99	1.02	1.00	1.00	1.00	0.99	1.00	0.99	1.00	1.00	0.99	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99
787.02		1.00	0.99	0.99	1.01	1.00	1.00	1.00	0.99	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	0.99	1.00	1.00	0.99
787.78		1.00	0.99	0.99	1.01	1.00	1.00	1.00	0.99	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	0.99	1.00	1.00	0.99	1.00	1.00	0.99
788.54		1.00	0.99	0.99	1.01	1.00	1.00	1.00	0.99	1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	0.99	1.00	1.00	0.99
789.30		1.00	0.99	0.99	1.01	1.00	1.00	0.99	0.98	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	0.99	1.00	1.00	0.99
790.06		1.00	0.99	0.99	1.02	1.00	1.00	1.00	0.98	1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	0.99	1.00	1.00	0.99
790.82		1.00	0.99	0.99	1.02	1.00	1.00	1.00	0.98	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99
791.58		1.00	0.99	1.00	1.02	1.00	1.00	1.00	0.98	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99
792.34		1.00	0.99	1.00	1.02	1.00	1.00	1.00	0.98	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99
793.10		1.00	0.99	1.00	1.02	1.00	1.00	1.00	0.98	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99
793.86		1.00	0.99	1.00	1.02	1.00	1.00	1.00	0.98	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	0.99
794.61		1.00	0.99	1.00	1.02	1.00	1.00	1.00	0.98	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
795.37		1.00	0.99	1.00	1.02	1.00	1.00	1.00	0.98	1.01	0.99	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
796.13		1.00	0.99	1.00	1.02	1.00	1.00	1.00	0.99	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
796.89		1.00	0.99	1.00	1.01	1.00	1.00	1.00	0.99	1.01	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
797.65		1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99
798.41		1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
799.17		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
799.93		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
800.68		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

***Key**

Bat ID	**Species**
1	*Plecotus auritus* 1
2	*Plecotus auritus* 2
3	*Plecotus auritus* 3
4	*Plecotus auritus* 4
5	*Plecotus auritus* 5
6	*Plecotus auritus* 6
7	*Pipistrellus pipistrellus* 1
8	*Pipistrellus pipistrellus* 2
9	*Pipistrellus pipistrellus* 3
10	*Pipistrellus pipistrellus* 4
11	*Pipistrellus pipistrellus* 5
12	*Pipistrellus pipistrellus* 6
13	*Pipistrellus pipistrellus* 7
14	*Pipistrellus pipistrellus* 8
15	*Pipistrellus pipistrellus* 9
16	*Pipistrellus pipistrellus* 10
17	*Rhinolophus ferrumequinum* 1
18	*Rhinolophus ferrumequinum* 2
19	*Myotis nattereri* 1
20	*Myotis nattereri* 2
21	*Myotis nattereri* 3
22	*Eptesicus serotinus*
23	*Pipistrellus pygmaeus*
24	*Myotis mystacinus* 1
25	*Myotis mystacinus* 2

Chapter 5: General Discussion

5.1. Summary of results

Globally, there has been a large shift from the use of gas discharge lamps to solid-state lighting technologies, predominantly LED lights. In 2016 the global LED lighting industry had a market value estimated to be worth 26.09 billion USD and in 2022 this is predicted to increase to 54.28 billion USD (Zion Market Research 2017).

Although LED lights have already been installed in a large number of towns and cities across the world, there has been limited research on the ecological impact of this switch-over in lighting technology. In chapter two, I addressed this in part by investigating how the switch-over of street lights from older lighting technologies, such as LPS and HPS lights to LED lights affected local bat activity. Encouragingly, I found this switch-over had little impact on the number of bat passes, i.e. bat activity at LED lights was not significantly different from that at LPS lights. Buzz ratios and insect activity also did not differ between the two types of street lights: although LED lights contain a higher proportion of short wavelengths compared to LPS lights, as neither emits UV wavelengths, it is likely that both lights are equally attractive to insects (Blake *et al.* 1994). So far studies have only compared insect attraction between HPS and LED lights: none have determined if there are any differences between LPS and LED. The results of these studies are mixed; in New Zealand, 48% more insects were attracted to LED lights compared to HPS lights (Pawson & Bader 2014), whereas in Germany significantly more insects were attracted to HPS compared to LED lights (Eisenbeis & Eick 2011). However, a more recent study in England found no significant difference between the number of insects attracted to LED and HPS lights (Wakefield *et al.* 2017).

My results complement those from similar switch-over studies; Stone *et al.* (2015) found that changing street lights from LPS to MH lights significantly increased the activity of *Nyctalus/Eptesicus* spp*., P. pipistrellus* and *P. pygmaeus*. This is most likely due to the UV component of the MH light, which is highly attractive to insects, and the bats that then prey on these insects, the attraction-by-insects-hypothesis

(Voigt *et al.* 2017). Moreover, Lewanzik & Voigt (2017) found that a switch-over from HPMV to LED lights caused a decrease in the activity of light-opportunistic species such as *P. pipistrellus*, but an increase in the activity of light-averse bats such as *Myotis* spp. Unlike the HPMV lights, LED lights do not contain UV emissions, and so are probably less attractive to insects and the light-opportunistic bats that often prey on them. The lack of UV wavelengths emitted from LED lights may also make them less visually disturbing to *Myotis* spp. than HPMV street lights, which would explain the increase in activity of *Myotis* spp. at LED lights. As *Myotis* spp. tend to pass by street lights while commuting, as opposed to feeding on the accumulation of insects attracted to the light due to the perceived risk of predation; switching to LED lights might allow these light-averse species to fly in closer proximity to street lights. This could increase the potential number of commuting and foraging routes for *Myotis* spp., possibly increasing their habitat range (Lewanzik & Voigt 2017).

Chapter two highlights that to fully understand the effects of ALAN on bats, it is essential to consider the spectral output of the artificial light. Spectral distribution measurements can only be achieved by using radiometric, rather than photometric recordings, even though the latter are often used in the literature. This chapter also emphasizes the importance of recording insect activity, as the behaviour of insects often underpins that of the bats, particularly for light-opportunistic bat species.

As well as installing LED street lights, many local authorities are also implementing a number of cost-saving strategies such as part-night lighting (PNL) and dimming (Azam *et al.* 2015; Day *et al.* 2015). PNL schemes appear to have limited ecological benefits due to the mismatch between the peak activity of bats (30 minutes - 1 hour after sunset) and the time the street lights are switched off (typically midnight – 5 am) (Stone 2013). However, there may be scope for dimming schemes to benefit bats by increasing the number of dark refuges they can use for commuting and foraging. In chapter three I investigated the effect of dimming on bat activity by exploring how four lighting levels (0%, 25%, 50% and 100% of the original output) affected both light-opportunistic and light-averse bat species. As expected, the higher light intensities benefited the light-opportunistic bats and negatively affected the light-averse species. The most interesting and promising result from a conservation perspective was that, in suburban areas, the low lighting level (25%, that was

equivalent to ~11.35 lux), did not have a significant effect on the activity of either the light-opportunistic or the light-averse bat species. These results contrast with an earlier study that explored dimming in rural areas in south-west England and found that even lux levels as low as 3.6 negatively affected the activity of the light-averse bats *Myotis* spp. and *R. hipposideros* (Stone, Jones & Harris 2012). These differences could be explained by the habitats where the two experiments were conducted. My study took place in suburban habitats, using existing street lights that have been installed for decades, so it is likely that local bat populations had adapted to the presence of lights. Conversely, Stone, Jones & Harris (2012) set up experimental street lights in rural areas that were previously unlit, so the local bat populations were not used to artificial light exposure. Perhaps, if the experimental street lights in rural habitats were installed for a longer period of time, bats could habituate to the artificial lights, resulting in similar behavioural responses to the ones I recorded. Moreover, the differences between our studies could also be because light-averse species, such as *Myotis* spp. are less likely to forage and commute in suburban habitats, preferring rural habitats that tend to be less open and in close proximity to vegetation clutter (Norberg & Rayner 1987). Encouragingly, my results suggest it might be possible to achieve a lighting level that is viable for humans, but also has ecological and economic benefits, at least in a suburban context.

Chapter three demonstrates that to gain a more comprehensive understanding of the ecological effects of dimming street lights, future research needs to consider the effects of dimming on both light-opportunistic and light-averse bat species in a range of different habitat settings, i.e. rural, suburban and urban areas.

Although the general trend is to switch street from LPS, HPS or HPMV to LED lights, other broad-spectrum technologies, such as fluorescent (FL) and metal halide (MH) street lights are also being installed. Both FL and MH lights have high CRI properties and are cheaper to install than LED lights (Williams 2009; Stone, Jones & Harris 2012). However, unlike LED lights, both FL and MH lights emit UV wavelengths, which may cause the light to be more visually disturbing, particularly for light-averse species (Lewanzik & Voigt 2017). UV vision is not as well understood in bats, particularly insectivorous species, compared to other taxa. In chapter four, I compared the UV transmission of lenses from a number of light-averse and light-

opportunistic bat species. I found there was no significant difference between the UV transmission of lenses from light-opportunistic and light-averse species. My results, in collaboration with molecular and behavioural studies, provide a strong case for UV vision in many species of insectivorous vespertilionid bats, which has important implications for street lighting initiatives, namely that the switch-over to LED lights seems more “ecologically” friendly than using either FL or MH lights.

5.2. Limitations of study

The main limitations of my study were that since I set up an *in-situ* experiment using existing street lights, I was unable to control for every variable. For example, in chapter two, there were differences in the intensity and power measurements between sites. My choice of sites was directed by which areas the local authorities were switching from LPS to LED street lights within the period that corresponded to peak bat activity. It is possible that the variation in intensity and power affected bat activity but teasing out how bats and even insects are affected by changes in intensity, given that it was measured as illuminance, a metric based on human vision, is very challenging, perhaps impossible. As explained in chapter two, local authorities were replacing the LPS street lights with LED lights that were deemed equivalent according to human needs and it seemed more appropriate for me to collect data using existing street lights, rather than setting up lighting installations myself, to ensure that my results were directly applicable to local authorities.

Furthermore, as my research was focused in suburban habitats, which are typically in more open areas with less vegetation clutter, this reduced the potential number of bat species that could be recorded. The majority of bat passes I recorded were of light-opportunistic, rather than light-averse, species. As light-averse bat species are typically rarer and of conservation concern it would have been useful to collect more data on these species to further our understanding on the ecological effects of ALAN. However, since it was important that my results are relevant to local authorities, I think it was more useful to investigate the effects of street lights on bat species that are most likely to be found in close vicinity to street lights, rather than setting up street lights in rural habitats, where artificial lights are unlikely to be

installed. Furthermore, as much of the previous literature has been focussed on the effects of street lighting on bats in rural settings (Stone, Jones & Harris 2009, 2012), investigating bats in suburban habitats was a novel approach and therefore expands our overall knowledge of the effects of ALAN on bats.

Finally, in chapter four, I required more samples of rhinolophid bat species to determine if there was a difference in the UV transmission of vespertilionid and rhinolophid bats. As rhinolophid species do not seem to have a functional UV tuned SWS visual pigment, it seems plausible that their lenses have lower UV transmissions than vespertilionid bats. As explained in chapter four, this hypothesis was not possible to test statistically due to the opportunistic way the data were collected i.e. using bat carcasses that were provided by bat carers and hospitals.

5.3. Recommendations

ALAN is a key anthropogenic stressor and so should be one of the focal points of global change research (Davies & Smyth 2018). Based on the results from my own research and relevant studies published in the literature, here are my recommendations to reduce the ecological impacts of street lights. My recommendations are focussed on bats, as they were my principal study taxon, but I will also consider other nocturnal taxa, many of which exhibit varying responses to ALAN.

5.3.1. Avoid unnecessary lighting installations

As bats have adapted to nocturnal lifestyles over millions of years, overall lighting has a negative impact on all bat species (Voigt *et al.* 2018). This is because even bat species that are termed light-opportunistic avoid lit areas at the landscape level (Hale *et al.* 2015; Azam *et al.* 2016; Pauwels *et al.* 2019). All bat species are light-averse when it comes to daytime roosts, drinking and hibernacula (Voigt *et al.* 2018). Waterways, such as streams and rivers are key drinking sites for bats and any artificial lighting seems to negatively affect all species, even the light-opportunistic *Pipistrellus kuhlii* (Russo *et al.* 2017). Ideally, it would be beneficial to reduce artificial lights by either removing existing artificial lighting installations or slowing down the

current rate of growth (Falchi *et al.* 2011). However, this is not possible in many areas due to human needs, such as a perceived sense of enhanced security, so lighting installations should be carefully considered in protected areas, locations in close proximity to roosting sites (both hibernacula and summer roosts) and habitats that light-averse species use to forage (Voigt *et al.* 2018). Outdoor lighting should also be at least 25m from vegetation and 45m from riverbanks to reduce its effects on insects (Perkin, Hölker & Tockner 2014; Degen *et al.* 2016) as this will affect the bats that prey on them.

5.3.2. Appropriate light design

Street lights should be designed to reduce as much light trespass as possible, i.e. the amount of superfluous light emitted from the luminaire. This could help reduce ALAN and have positive effects on local ecosystems by reducing spill-over to important foraging and commuting habitats (Falchi *et al.* 2011; Gaston *et al.* 2012; Voigt *et al.* 2018): reducing light trespass is important in maintaining the activity of light-averse *Myotis* spp. (Azam *et al.* 2018). Luminaires should be positioned at the correct height, so they do not emit any light at or above the horizontal i.e. at 0 – 45^{o} from the horizontal plane (Falchi 2011). Poor luminaire design can exacerbate the ecological impact of street lights by increasing the visibility of the light source in a landscape, which could interfere with the commuting and foraging of more species and the amount of sky glow (Gaston *et al.* 2012). Positioning street lights at the correct column height and using effective shielding fixtures and baffling can also reduce unwanted light emissions (Falchi *et al.* 2011).

5.3.3. Use of LED street lights

Where street lighting is unavoidable, LED lights should be installed in preference to other lighting technologies since they have multiple economic, environmental and visual benefits for humans, and seem to be the most “ecologically” friendly street light. This is because, unlike other broad-spectrum technologies such as FL and MH lights, LEDs do not emit UV wavelengths, which seem to be the most disruptive to a number of species (Lewanzik & Voigt 2017; Wakefield *et al.* 2017). LED lights are also highly controllable and flexible, so can be easily customised to accommodate their surroundings. Moreover, LED lights produce more directional light by focusing

the light downwards, thereby reducing the amount of light emitted at or above the horizontal (Gaston *et al.* 2012), again reducing the ecological impacts of ALAN.

5.3.4. Spectral tuning

As well as UV wavelengths, shortwave emissions, such as those in the blue part of the spectrum, seem to be the most detrimental for ecological systems, human health and astronomy (Falchi *et al.* 2011). Short wavelengths, particularly for invertebrates, tend to correspond with the peak sensitivities of the photoreceptor cells in their eyes (Muirhead-Thomson 1991; Eisenbeis 2006; Cowan & Gries 2009). Moreover, blue light can also suppress melatonin production, a key hormone in regulating circadian rhythms. Interruption to melatonin production could have negative effects on other key physiological systems, such as metabolism, sleep-cycles, immunity, reproduction and migration (Navara & Nelson 2007). Furthermore, Rayleigh scattering of short wavelengths means that blue light creates more light pollution than longer wavelengths, such as green or red light (Falchi *et al.* 2011).

The advantage of LED lights is that their spectral output can be manipulated depending on the surrounding taxa, so LED lights can be tuned to reduce the amount of blue light emitted. LED lights are typically sold as cool (~5000 K), neutral (~4000 K) and warm (~2700 K), with the proportion of blue wavelengths reducing as the CCT decreases, i.e. the artificial light seems warmer in appearance (Longcore *et al.* 2015). However, the colour temperatures of LED lights can also be customised. A study compared the attraction of insects to three customisable LED lamps (3510, 274 and 2728 K), as well as two off-the-shelf LED lamps (2700 K from two different manufacturers), found that spectral composition had a significant effect on invertebrate activity. The custom 3510 K LED lights attracted more arthropods than the commercial 2700 K LED lights, as well as the custom 2704 and 2728 K LED lights (Longcore *et al.* 2015). LED lights that emit fewer short wavelengths attract fewer insects and so could help to reduce the advantage that light-opportunistic bats have over light-averse bat species, potentially realigning the balance between these two bat groups. The only drawback of manipulating the light spectra to reduce insect attraction and the bats that prey on them is that there may be some sacrifices in terms of CRI and lamp efficiency, which have implications for human vision and financial viability (Longcore *et al.* 2015).

As well as modifying the CCT, LED lights can also be designed to be radically different colours. An ongoing study in the Netherlands investigating the long-term effects of spectral composition of white, green (increased blue and reduced red wavelengths) and red (increased red and reduced blue wavelengths) found that the effect of spectral composition varied with species. Light-opportunistic bats such as *Pipistrellus* spp. increased their activity at white compared to red light, whereas light-averse bats, such as *Myotis* and *Plecotus* spp., increased activity at red compared to green or white lights (Spoelstra *et al.* 2015, 2017). Based on the results of this study, red LED lights have been installed in parts of Barneveld, a town in the Netherlands with important bat foraging and commuting routes (Dutch News 2018). However, this has not been popular with local residents, emphasising the importance of raising the awareness of the ecological impacts of street lighting to the general public (Hölker *et al.* 2010a). Moreover, red light does not seem to be tolerated by light-averse *Rhinolophus hipposideros*, which may be more sensitive to ALAN than *Myotis* spp., highlighting that it is not possible to use a one-size-fits-all approach (Zeale *et al.* 2018).

As well as public opposition to drastic alterations in the spectral output of street lights, lighting manufacturers are also unlikely to want to make such changes, as the enhanced CRI properties of broad spectrum “white” lights is a main selling point and so any significant spectral changes could undermine their profits (Davies & Smyth 2018). Furthermore, many of the studies investigating how manipulating the spectral output could help mitigate the ecological effects of ALAN do not use a consistent approach, making it hard to disentangle the effects of spectral changes (Davies & Smyth 2018). It is also very difficult to achieve a light spectrum that is appropriate for human vision, while reducing the ecological impact, as the responses to different spectral outputs varies across taxa (Davies & Smyth 2018). For example, red light positively affected the growth of male caterpillars of the moth *Mamestra brassicae* (van Geffen *et al.* 2014), but negatively affected the mating behaviour of the winter moth *Operophtera brumata* (van Geffen *et al.* 2015). Moreover, although red light might be beneficial for a number of taxa, it has profound negative effects on others, such as migrating birds (Deutschlander, Phillips & Borland 1999; Gauthreaux & Belser 2006; Poot *et al.* 2008), where shorter wavelengths seem to be more beneficial. For example, illuminating power lines with UV light reduced the number of

collisions of crane species by 98% (Dwyer *et al*. 2019). However, overall it seems that as short wavelengths, particularly in the blue spectrum, have the propensity to affect so many organisms, LED lights should be tuned to reduce these emissions as much as possible, so that they only emit wavelengths above 540 nm (Falchi *et al.* 2011).

5.3.5. Implement mitigating strategies

Mitigation strategies are often employed by local authorities because they can reduce the running costs of street lights, but they may also be beneficial to a number of nocturnal taxa (Gaston *et al.* 2012). As well as dimming and PNL schemes, a number of other intelligent lighting schemes are being introduced, such as the use of motion sensors (Falchi *et al.* 2016). These ensure that street lights are only switched on when necessary. It is, however, unknown if these fluctuations in lighting levels affect bat activity (Longcore & Rich 2004; Royal Commission on Environmental Pollution 2009). While PNL schemes have limited success for bats due to the mismatch between the timing of the light being switched off and the peak nightly bat activity, these schemes could be effective for other taxa, such as nocturnal invertebrates. Dimming the light to 50% of its original output (< 14 lux), and switching it off between midnight and 4 am, is an effective strategy to reduce the effect of ALAN on invertebrates (Davies *et al.* 2017).

Dimming schemes could also help minimize the ecological impact of ALAN on bats. If the amount of light distributed from the light source is reduced, this could create dark refuges that light-averse bats could use to commute and forage across a landscape. This might allow light-averse species to utilise areas that they typically avoid due to the perceived risk of predation, potentially enabling them to find more efficient commuting routes and profitable foraging habitats. This ultimately could reduce the competitive advantage light-opportunistic bats have over light-averse bats in suburban and urban areas (Lewanzik & Voigt 2017). For dimming to be an effective mitigation strategy, there needs to be a balance between finding an adequate light level for human vision and a light level that has the fewest negative impacts on light-averse bat species. To achieve this light intensity, further research is required to investigate the effects of dimming of bats in rural, suburban and urban habitats. This is because a study in a rural habitat found that very low light levels (<

3.6 lux) negatively affected the activity of light-averse species (Stone, Jones & Harris 2012), whereas in suburban habitats, reducing the light intensity of street lights to 25% of its original output (~11.35 lux) did not have a negative impact on the activity of light-averse species (Rowse, Harris & Jones 2018).

Vegetation refuges, such as those provided by tree cover are important for habitat connectivity and could help to reduce the negative effects of artificial lighting, such as increased predation risk (Mathews *et al.* 2015; Straka *et al.* 2019). Installing screens, by planting hedgerows and trees could reduce the amount of light trespass from the light source to the nearby habitats (Voigt *et al.* 2018).

5.4. Future directions of research

With increasing research and awareness on the ecological effects of ALAN, some countries have decreased the amount of artificial lighting produced. For example, between 1992 and 2009 Canada and the United Kingdom have reduced brightly lit areas by 34% and 17% respectively (Cauwels, Pestalozzi & Sornette 2014; Davies *et al.* 2014; Elvidge *et al.* 2014). Schemes such as the International Dark Sky Association work with a range of stakeholders, such as policymakers, lighting manufacturers and the public, provide resources to decrease the amount of light pollution (Koen *et al.* 2018). However, there is still a long way to go to reduce ALAN and its ecological effects; below I summarise some areas for future research.

5.4.1. Long-term studies

The majority of studies focussing on the ecological impacts of ALAN are short-term and are set up in rural locations, where street lights are very unlikely to be installed as they are not in close vicinity to human activity. It is unknown if effects, including delayed emergence from roost (Downs *et al.* 2003), roost abandonment (Boldogh, Dobrosi & Samu 2007), reduced commuting possibilities (Stone, Jones & Harris 2009, 2012), increased foraging for light-opportunistic species (Rydell 1992; Blake *et al.* 1994) and reduced foraging for light-averse species (Polak *et al.* 2011), are short-term or will have lasting behavioural and even fitness consequences. There are only two examples of long-term studies in the literature; one study compared the number

of bat colonies of *Plecotus auritus* at 61 churches in Sweden in the 1980s, with those present in 2016, when half of the churches were lit with aesthetic, exterior building lighting (Rydell *et al.* 2017). Over that period, there was a 38% reduction in the number of bat colonies, which is likely to be caused by the introduction of lights. The other, an experiment in the Netherlands, is exploring the effects of three types of LED lights on a range of taxa over a five year period (see section 5.2.3 for more details) (Spoelstra *et al.* 2015, 2017). Although this experiment should determine the long-term behavioural effects of ALAN on a range of species, it is of limited value to local authorities, many of which are under financial pressure to implement cost saving strategies immediately. This highlights the importance of trying to strike the balance between collecting enough data to make accurate recommendations and the speed in which the data can be collected.

5.4.2. Fitness consequences

In terms of reducing the impacts of ALAN on bats, which are slow reproducing mammals, it is important to understand if there are long-term fitness consequences. Many bat species seem to alter their behavioural responses to ALAN, but as yet we do not know if these behavioural changes translate into fitness effects (Voigt *et al.* 2018). The only study to explore the potential fitness effects of bats showed that juvenile *Myotis* spp. roosting in illuminated buildings had a lower mass than those bats roosting in unlit buildings (Boldogh, Dobrosi & Samu 2007). However, this study did not determine if these differences in mass of the juvenile bats in lit roosts resulted in reduced survival rate after hibernation. A recent study used radio-tracking data from *Rhinolophus hipposideros* to determine fitness proxies, such as ranging behaviour and habitat use (Zeale *et al.* 2018). Four street lights with different spectral outputs (LED, HPS, red and green induction lights) were situated along hedgerows used for commuting from maternity roosts to determine how the presence of these lights affected the movement of these light-averse bats. Although the activity of *R. hipposideros* was reduced significantly when any of the street lights were switched on, the bats quickly modified their behaviour by flying along the opposite side of the hedge that was not lit. Encouragingly, the radio-tracking data revealed that the street lights did not have any effect on either home range size or habitat preferences. If these metrics are good fitness proxies, then these results

demonstrate that the effect of ALAN on light-averse species can be mitigated if there are alternative routes available. However, it is important that these routes are suitable for these bat species, i.e. by providing sufficient protection from light (both natural and artificial), as well as enabling the bats to fly similar distances from their roost to avoid any increases in energy expenditure.

5.4.3. Community level effects

To gain a further understanding of the ecological impacts of ALAN, in addition to exploring the effects of different species within a taxon, research needs to start investigating the impact across multiple taxa at varying trophic levels. Bats do not exist in isolation, so it is important to consider the effects of ALAN on vegetation, invertebrate and vertebrate activity. The effects of ALAN at the community level are already starting to be explored in insects; the reduced visitation rates of nocturnal pollinators at lit, compared to unlit, plant sites found that reduced reproductive success of plants could not be offset by diurnal pollinators (Knop *et al.* 2017).

5.4.4. Landscape level effects

Many studies investigating the ecological impacts of ALAN only consider biodiversity at a local scale, using a few street lights (Rich & Longcore 2006; Stone, Jones & Harris 2012; de Jong *et al*. 2015). However, it is important to understand if these small-scale changes have landscape-level effects (Azam *et al.* 2016). It is essential that local-scale experiments are considered in their landscape context, because the effect of a small lit section in a dark rural habitat may be negligible for a number of bat species, but a lit section in a highly lit urban area may be enough to deter bats. This could affect their commuting and foraging behaviour, potentially having detrimental long-term impacts (Hale *et al.* 2015). However, street lights can also increase the activity of light-opportunistic species, thereby potentially creating predictable foraging patches. ALAN has also been shown to inhibit the gap crossing behaviour of light-opportunistic species (Hale *et al.* 2015). A study in France found that at a landscape scale, ALAN can result in habitat fragmentation, which affects all bat species, regardless of their foraging behaviour around street lights. It seems even light-opportunistic species are either negatively or neutrally affected by artificial lighting (Azam *et al.* 2016).

5.4.5. Bat vision

To better understand the effect of ALAN on bat activity, further research is required on bat vision, particularly obtaining the spectral sensitivities of different species. More information on spectral sensitivity at the neural processing level would be useful in order to determine whether species with UV transmissive lenses actually perceive UV wavelengths. More detailed information on UV sensitivity and UV vision in bats would aid street lighting strategies, primarily the intensity levels and spectral tuning of street lights (Gaston *et al.* 2012; Voigt *et al.* 2018). These data could be particularly useful in further understanding the effects of street lights on light-averse bats, who avoid lit areas even when there is an increased insect abundance.

5.4.6. Future lighting

In addition to continuing to explore how adaptive and intelligent technologies, such as motion sensors and money-saving lighting strategies such as dimming and PNL could help to mitigate the detrimental ecological effects of ALAN. It is important that the academic community, with the help of lighting developers and engineers, are aware of future lighting technologies, and explore their impacts before the technologies are installed. The switch-over to LED lights from older gas discharge lights started before the effects on ecological systems were understood, and in fact there are still many unknown effects of LED lights on a range of taxa. It is essential for conservation biology research to stay at the forefront of lighting developments rather than investigate their impacts retrospectively (Pawson & Bader 2014). The successors of the LED lights are predicted to be laser diodes, which are smaller than LED lights, more energy efficient and have increased longevity. Since laser diodes have already started to be installed in vehicles (Jef 2014), biologists need to explore their ecological impacts now to see if their effects differ from those of LED lights.

5.4.7. Measuring light

The intensity of street lights is often described in terms of illuminance, which is measured in lux. This is an appropriate unit in the lighting industry as the brightness of the light is adjusted to the spectral sensitivity of human eyes and ultimately street lights exist for human needs. However most taxa, including bats and insects, have

different spectral sensitivities, which means that lux readings do not encompass all the necessary biological information (Longcore & Rich 2004). For example, two broad spectrum light sources, such as MH and LED street lights, both have an illuminance of 50 lux and so are seemingly equivalent lighting sources. However, as spectral output influences the effects of ALAN on a number of organisms (Stone *et al*. 2015; Lewanzik & Voigt 2016; Wakefield *et al*. 2017), and as MH emit UV wavelengths, these lights could have profoundly difference effects on the surrounding fauna compared to LED lights, even though they have comparable lux values. Moving forward, it is therefore important to collaborate with scientists and lighting engineers to develop a system of measuring light, which includes spectral sensitivity information from a range of nocturnal taxa (Longcore & Rich 2004).

5.5. Conclusion and final comments

ALAN is going to continue to grow and therefore has the potential to be an increasing threat to biodiversity over the next century. In terms of moving forward, it is important that there is a collaborative approach amongst multiple stakeholders, including local authorities, industrial partners, lighting developers, policymakers and scientists to minimise the impact of ALAN on biodiversity, CO_2 emission and human health, as well as being cost effective (Hölker *et al.* 2010a; Gaston *et al.* 2012; Stone, Jones & Harris 2012).

At a landscape level, all bats are light-averse and will avoid street lights when commuting. Light-opportunistic bats use of artificial lighting seems dependent on a cost-benefit analysis approach, i.e. if the benefit of catching a prey item outweighs the cost of predation. Therefore, artificial lighting should be avoided, although, with increasing urbanisation and industrialisation taking place in towns and cities in developing, as well as developed countries, this is not feasible due to safety and security concerns (Cinzano, Falchi & Elvidge 2001; Gaston *et al.* 2012). Where artificial lighting is obligatory, my results, in combination with those from the current literature, suggest that LED lights should be used in preference to any other broad-spectrum lighting technology. As well as providing environmental benefits such as reducing greenhouse gas emissions and increasing energy efficiency, LED lights

have significant financial benefits such as controllability over light duration and intensity, increasing colour rendering properties, and reduced running costs (Elvidge *et al.* 2010; Hölker *et al.* 2010b; De Almeida *et al.* 2014). LED lights also seem to be the most “ecologically” friendly lighting technology, mainly because of their adaptability, making it possible to employ a myriad of strategies that could be beneficial for a number of species.

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Appendix I

Chapter 7
Dark Matters: The Effects of Artificial Lighting on Bats

E.G. Rowse, D. Lewanzik, E.L. Stone, S. Harris and G. Jones

Abstract While artificial lighting is a major component of global change, its biological impacts have only recently been recognised. Artificial lighting attracts and repels animals in taxon-specific ways and affects physiological processes. Being nocturnal, bats are likely to be strongly affected by artificial lighting. Moreover, many species of bats are insectivorous, and insects are also strongly influenced by lighting. Lighting technologies are changing rapidly, with the use of light-emitting diode (LED) lamps increasing. Impacts on bats and their prey depend on the light spectra produced by street lights: ultraviolet (UV) wavelengths attract more insects and consequently insectivorous bats. Bat responses to lighting are species-specific and reflect differences in flight morphology and performance: fast-flying aerial hawking species frequently feed around street lights, whereas relatively slow-flying bats that forage in more confined spaces are often light-averse. Both high-pressure sodium and LED lights reduce commuting activity by clutter-tolerant bats of the genera *Myotis* and *Rhinolophus*, and these bats still avoided LED lights when dimmed. Light-induced reductions in the activity of frugivorous bats may affect ecosystem services by reducing dispersal of the seeds of pioneer plants and hence reforestation. Rapid changes in street lighting offer the potential to explore

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mitigation methods such as part-night lighting (PNL), dimming, directed lighting, and motion-sensitive lighting that may have beneficial consequences for light-averse bat species.

7.1 Introduction

Anthropogenic change is altering ecosystems at unprecedented rates and humans now dominate most ecosystems (Vitousek et al. 1997; McDonald 2008). Urbanisation in particular has major impacts on bat activity and abundance (Jung and Threlfall 2016), and one aspect of global change that occurs predominately, but not exclusively, in urban areas is increased artificial light at night. Almost a fifth of the global land area was affected by light pollution in 2001 (Cinzano et al. 2001). Although night-time brightness generally increased in Europe between 1995 and 2010, regional patterns are complex, with some localised declines (Bennie et al. 2014). However, the biological impacts of light pollution have only recently been recognised (Longcore and Rich 2004).

Being nocturnal, bats are likely to be affected by light pollution. In this chapter, we review the types of artificial light that bats experience, describe how light pollution has become more widespread in recent years, show how technological changes may lead to significant reductions in light pollution and describe some of the physiological consequences of light pollution that may be relevant to bats. We then discuss how artificial lighting affects the insect prey of bats, and why some bats may benefit from the growth in artificial lighting, whereas others are affected detrimentally. After highlighting some aspects of bat vision, we describe the shift from observational to experimental studies of how bats respond to lighting. Finally, we identify some of the major knowledge gaps and suggest priorities for future research on the effects of artificial lighting on bats.

7.2 Types of Artificial Light

The electromagnetic spectrum encompasses radiation with wavelengths ranging from less than a nanometre (gamma rays) to a kilometre (radio waves) (Campbell 2011). While humans perceive wavelengths between 400 and 700 nm as 'visible light' (Purves and Lotto 2003), birds, fish and invertebrates can detect light in the ultraviolet (UV) range (10–400 nm). Recent work suggests that UV sensitivity may be widespread among mammals (Douglas and Jeffery 2014), and snakes and beetles can detect spectral emissions in the infrared range (700–1000 nm) (Schmitz and Bleckmann 1998; Land and Nilsson 2012).

Artificial lighting has infiltrated all aspects of human life both indoors and outside (Gaston et al. 2012). Here, we focus on street lighting because of its universal use and potential for ecological impacts (Gaston et al. 2012). Different types of street light have distinct spectral signatures (Fig. 7.1); their primary emissions

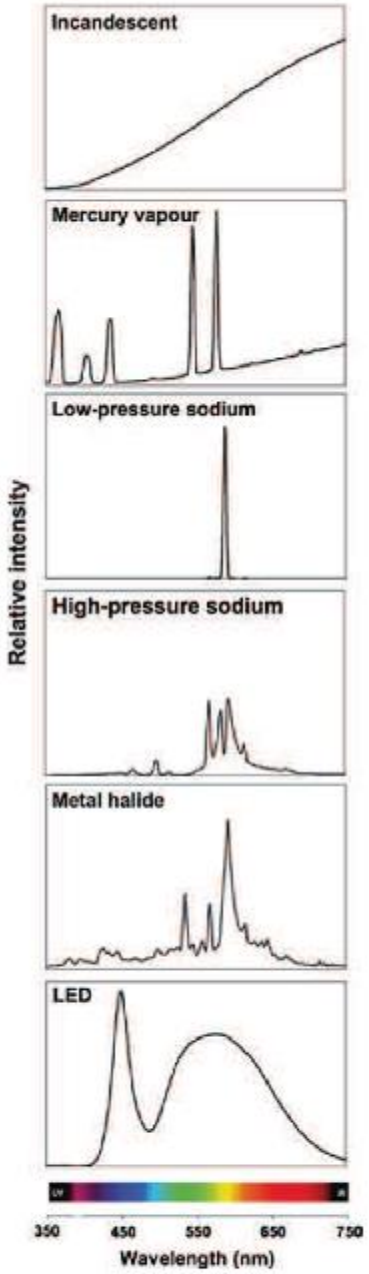

Fig. 7.1 The spectral content of different light types varies considerably. The spectral composition of common lighting technologies is shown. From Gaston et al. (2013)

depend on the type of reactive material or coating in the lamps (Buchanan 2006). Incandescent lamps, developed by Thomas Edison in 1880, mainly emit long wavelengths with a maximum intensity between 900 and 1050 nm (Elvidge et al. 2010). Despite improvements such as the quartz halogen lamp, which uses an inert gas to preserve the tungsten filament, incandescent lamps are still relatively inefficient because their emissions are predominantly near the infrared spectrum and so largely invisible to humans (Elvidge et al. 2010).

Gas discharge lamps, developed by the mid-twentieth century, produce light by passing electric arcs through gas-filled bulbs (Elvidge et al. 2010). These are further classified as low-pressure discharge and high-intensity discharge (HID) lamps (Elvidge et al. 2010). Low-pressure discharge lamps include the compact fluorescent lamp (CFL) and low-pressure sodium (LPS) lamps. Fluorescent lamps produce distinct emission peaks, which combine to emit a 'white' light (Royal Commission on Environmental Pollution 2009; Elvidge et al. 2010), whereas LPS lamps have a narrow spectral signature, emitting monochromatic orange light with a peak intensity of 589 nm (Fig. 7.1) (Rydell 2006; Elvidge et al. 2010).

HID lamps include high-pressure mercury vapour (HPMV) lamps, which produce a bluish-white light, and high-pressure sodium (HPS) and metal halide lamps that have broader spectral emissions (Fig. 7.1) (Davies et al. 2013). Emissions from HPMV lamps extend into the UV range (Rydell 2006; Elvidge et al. 2010), whereas HPS lamps emit yellow-orange light and metal halide lamps 'white' light (Royal Commission on Environmental Pollution 2009; Davies et al. 2013; Gaston et al. 2013). The colour rendering index (CRI) compares how accurately a light source replicates the full range of colours of an object viewed in natural light on a scale of 0–100, where 100 is equivalent to natural light (Schubert and Kim 2005; Elvidge et al. 2010; Davies et al. 2013). HPS lamps typically have a CRI between 7 and 32, whereas metal halide lamps have a CRI ranging from 64 to 100, reflecting their ability to render colour more suited for human vision (Elvidge et al. 2010; Gaston et al. 2012).

Gas discharge lamps replaced incandescent lamps because of their energy efficiency and improved longevity (Schubert and Kim 2005), and LPS (44 %) and HPS (41 %) lamps came to dominate street lighting in the UK (Royal Commission on Environmental Pollution 2009) and elsewhere. The luminous efficacy (LE) (amount of light produced per watt of electricity) of gas discharge lamps is five times higher than incandescent lamps (Schubert and Kim 2005; Elvidge et al. 2010). However, with pressure to reduce energy use and CO_2 emissions, the lighting industry is now turning to light-emitting diodes (LEDs) (Elvidge et al. 2010; Gaston et al. 2012). LEDs have broad spectral signatures, typically 400–700 nm, with very few emissions in the UV range (Elvidge et al. 2010). This is achieved mainly through the use of cerium-doped yttrium aluminium garnet (YAG:Ce) phosphors with a gallium nitride (GaN) which converts monochromatic blue to 'white' light. However, more recently LEDs are able to produce light by combining multiple monochromatic sources (red, green and blue), which allows for greater control over spectral emissions (Narendran et al. 2004; Gaston et al. 2012, 2013; Davies et al. 2013). LED lamps have comparable CRI scores to metal

halide lamps (65–100) (Elvidge et al. 2010) but benefit from lower running costs (Gaston et al. 2012); low energy consumption (Elvidge et al. 2010); controllability of spectral, temporal and intensity of emissions; reduced CO_2 emissions (Hölker et al. 2010a); and smart lighting capabilities that enable dimming in response to weather, traffic and lunar conditions (Bennie et al. 2014).

7.3 The Growth of Light Pollution

Light pollution is defined as the changing of natural light levels in nocturnal landscapes (nightscapes) through artificial lighting sources (Falchi et al. 2011; Kyba and Hölker 2013). Here, we focus on ecological light pollution, i.e. the direct ecological effects of light as opposed to astronomical light pollution, which describes the light that disrupts viewing of stars and other celestial matter (Longcore and Rich 2004). Ecological light pollution can be caused by glare (extreme contrasts between bright and dark areas), over-illumination, light clutter (unnecessary numbers of light sources), light trespass (unwanted light) and skyglow, where artificial light is directed towards the sky, scattered by atmospheric molecules and reflected back to earth (Royal Commission on Environmental Pollution 2009; Gaston et al. 2012; Kyba and Hölker 2013).

Artificial lighting has increased as a result of urbanisation, population growth, economic development and advances in lighting technologies and provides numerous economic, commercial, recreational and security benefits (Riegel 1973; Hölker et al. 2010a; Davies et al. 2012). However, light pollution is now of global concern: the accelerated use of electric lighting, growing at 6 % per year, has escalated light pollution to threat status (Hölker et al. 2010a, b). Satellite images suggest that 19 % of the global land surface surpassed the threshold for acceptable lighting levels (Cinzano et al. 2001). However, satellites are unable to capture all illumination from light sources (Bennie et al. 2014). While light pollution is currently more apparent in developed nations (Fig. 7.2), projected increases in industrial and urban growth suggest that light pollution will become more spatially heterogeneous both locally and regionally (Cinzano et al. 2001; Gaston et al. 2012; Hölker et al. 2010b; Bennie et al. 2014).

In the UK, street lighting consumes approximately 114 Twh of energy annually (International Energy Agency 2006) and is growing at 3 % per annum (Royal Commission on Environmental Pollution 2009). The number of lighting installations is increasing (Gaston et al. 2012), and the change in emissions due to increased use of broad spectrum technologies is also likely to affect light pollution as these sources emit higher levels of blue light. This scatters more into the atmosphere than green or red light, ultimately making a bigger contribution to skyglow (Benenson et al. 2002; Falchi et al. 2011; Kyba and Hölker 2013). The growth in light pollution will be further exacerbated because, as LEDs become cheaper, non-essential uses, such as advertising and architectural lighting, may increase (Schubert and Kim 2005).

Fig. 7.2 Artificial lighting is currently most widespread in the developed world. Global use of lighting at night in 2000. From NASA Earth Observatory/NOAA NGDC (2012)

7.4 Projected Changes in Technology

International lighting policies are prioritising energy-efficient technologies to reduce costs and CO_2 emissions. The European Ecodesign Directive, for instance, encourages moves from energy-intensive technologies such as incandescent, LPS and HPMV lamps (Hölker et al. 2010a) to 'whiter' lighting with higher colour rendering capabilities (Gaston et al. 2012). This may reduce CO_2 emissions in the EU by as much as 42 Mt per year. A number of pilot studies in cities around the world (including Adelaide, Hong Kong, London, Mumbai, New York, Sydney and Toronto) have compared LED lamps against existing lighting technologies. After a three-year trial, the City of Sydney Council agreed to switch to LEDs on 6500 outdoor lights due to their reduced energy consumption, cost-effectiveness and improved illuminance (The Climate Group 2014).

Future research will focus on increasing the efficiencies of LEDs: the LE of a LED is 60–90 lm/W, compared to 80–120 lm/W for HPS lamps (California Lighting Technology Center 2010). More effective ways of producing light are also being investigated, such as combining multiple monochromatic sources as opposed to using phosphors: this will increase control over spectral emissions (Schubert and Kim 2005; Gaston et al. 2012).

7.5 The Biological Effects of Light Pollution

The number of studies revealing negative consequences of artificial night lighting on a multitude of both diurnal and nocturnal vertebrates and invertebrates is increasing rapidly (reviewed in Rich and Longcore 2006). Most negative effects

are due to the disruption of natural circadian and circannual cycles, which in turn can affect a whole range of species interactions, physiological processes and behaviours.

7.5.1 Impacts of Light Pollution on Intra- and Inter-specific Competition

Light-induced changes in circadian activity patterns can alter competition both within species (e.g. for mates) and between species (e.g. interference and exploitation competition). These are best documented for birds. For instance, early singing may be a signal of male quality in songbirds and increases the rate of extra-pair copulations, which are usually higher in older males. In territories affected by artificial light, males of several songbird species start singing earlier at dawn and thereby gain access to about twice as many extra-pair mates (Kempenaers et al. 2010; Nordt and Klenke 2013; Dominoni et al. 2014). The effect of artificial light on paternity gain is even stronger in yearlings than in adults, and so street lights might result in maladaptive mate choice of females by artificially increasing the extra-pair success of yearlings (Kempenaers et al. 2010). Whether similar maladaptive effects occur with nocturnal species is less clear.

Artificial light can affect niche partitioning by extending the activity of diurnal species, bringing them into inter-specific competition with nocturnal species (Longcore and Rich 2004; Rich and Longcore 2006). The scissor-tailed flycatcher *Tyrannus forficatus*, for example, will catch insects at street lights until at least 3 h after sunset (Frey 1993); this may increase exploitation and interference competition with insectivorous bats. Light pollution may also cause inter-specific competition between bats, with light-sensitive bat species excluded from illuminated resources exploited by light-tolerant species (Arlettaz et al. 2000).

7.5.2 Effects of Artificial Light on Physiological Homeostasis

Light-induced changes in circadian rhythms may induce physiological aberrations. For instance, exposure of captive mice to light at night disrupts metabolic signals, leading to increased body mass and decreased glucose tolerance (Fonken et al. 2010). Dim night-time light can also impair learning and memory, affect stress hormone levels, compromise immune function and cause depressive-like behaviour in rodents (Bedrosian et al. 2011, 2013; Fonken et al. 2012). In humans, depression, obesity and cancer risk relate to light pollution and associated disruptions of the circadian system (Fonken and Nelson 2011; Kronfeld-Schor and Einat 2012; Haim and Portnov 2013).

Light pollution can also result in a decoupling of seasonal behaviours and physiological adaptations from the optimal time of year. So, for instance, reproduction might be desynchronised from peak food availability; even very low light levels at night advance avian reproduction (Dominoni et al. 2013) so that birds breed earlier close to street lights than in darker territories (Kempenaers et al. 2010). Light-induced decoupling can even reverse an animal's seasonal phenotype, so that it exhibits a long-day phenotype in winter and vice versa. In sheep, 1 h of light during the dark phase is enough to mimic a long-day during short-day conditions (Chemineau et al. 1992). Also in primates, artificial light at night can induce a long-day phenotype; these animals had higher core body temperatures, showed less locomotor activity during the nocturnal activity period and had fainter torpor bouts compared with short-day photoperiod acclimated animals (Le Tallec et al. 2013). Voles that experienced light interference at night showed reduced winter acclimatisation of their thermoregulatory system to such a degree that they reduced heat production and died under winter field conditions (Haim et al. 2004, 2005). Thus, light pollution may have deleterious impacts on survival when animals expend too much energy during winter (Haim et al. 2004): this may be relevant for hibernating bats.

7.5.3 *Interference of Light Pollution with Nocturnal Navigation*

A well-documented effect of light pollution not mediated through circadian rhythms is the impact on movement decisions of visually orienting animals. Nesting attempts of female sea turtles are disrupted by artificial light, and light attracts or confuses the hatchlings, rendering them more vulnerable to predation, exhaustion and dehydration (Salmon 2006; Perry et al. 2008; Berry et al. 2013).

Birds migrating at night often approach bright lights instead of following their normal migration route, possibly because the light interferes with their magnetic compass (Poot et al. 2008). Birds may also be trapped within the sphere of light, milling around illuminated objects until they die through collisions or exhaustion (Gauthreaux and Belser 2006; Montevecchi 2006; Spoelstra and Visser 2014). This may have relevance to bats, which also use magnetic compasses for navigation (Holland et al. 2006).

Similarly many insects, particularly moths (Lepidoptera), use artificial lights rather than the moon for orientation and die of exhaustion when circling a lamp or following a collision with the hot cover. Artificial light also provokes a 'dazzling effect': many insects become immobilised when approaching a lamp and rest on the ground or in vegetation, becoming easy prey (Eisenbeis 2006). Light pollution may even be a driver of an insect biodiversity crisis (Conrad et al. 2006). The 'vacuum cleaner' effect, i.e. the long-distance attraction of light-susceptible species to lamps, removes large numbers of insects from the ecosystem, even

resulting in local extinctions. This flight-to-light behaviour strongly depends on spectral output of the lighting: white HPMV lamps have a high UV proportion of their spectrum, and so four times as many moths are captured at HPMV lights compared to yellow/orange HPS lights (Eisenbeis 2006). Warm-white and cool-white LED lights induce less flight-to-light behaviour than HPS lights (Huemer et al. 2010; Eisenbeis and Eick 2011), and the virtually monochromatic deep-orange LPS lights are least attractive to insects (Rydell 1992; Blake et al. 1994; Eisenbeis 2006; Frank 2006).

Several spiders, amphibians, reptiles, birds and bats focus their foraging on insects accumulated at street lights (Rich and Longcore 2006). For bats, this can also be advantageous because artificial light disrupts the evasive behaviour of most nocturnal Lepidoptera, rendering them more vulnerable to bat attacks (Svensson and Rydell 1998; Acharya and Fenton 1999).

7.6 Bat Vision

Vision is important in the lives of many bats; see reviews in Suthers (1970), Altringham and Fenton (2003) and Eklöf (2003). A number of species rely on vision to a large extent (Altringham 2011). Since vision is important to both bats and their predators, we briefly summarise some key recent findings relevant to bats' perception of artificial lighting.

Most pteropodids do not echolocate and use vision to locate fruit and flowers. Some echolocating bats use vision to complement auditory information when hunting (Eklöf and Jones 2003) and, if vision and echolocation provide conflicting information, visual information is used in preference (Orbach and Fenton 2010). Vision can also be more effective than echolocation over long distances (Boonman et al. 2013), and the California leaf-nosed bat *Macrotus californicus* relies more on vision when hunting prey under low levels of illumination equivalent to a moonlit night (Bell 1985).

Recent research on bat vision has focussed on the molecular evolution of light-sensitive pigments (Jones et al. 2013). As for most nocturnal mammals, bat retinas are dominated by rods: they are highly sensitive under low light and confer monochromatic vision. The opsin DNA sequences of rhodopsin (the opsin in rods) were intact in 15 bat species (Zhao et al. 2009a) and wavelengths of maximum absorbance were 497–501 nm.

Colour vision in mammals results in part from opsins in the cones that are sensitive to short and medium wavelengths. Zhao et al. (2009b) sequenced a short-wavelength sensitive opsin gene (*Sws1*) that is most sensitive to blue-violet wavelengths, and a medium-to-long-wavelength sensitive opsin gene (*M/lws*) in a range of bat species; maximum absorbance of red light wavelengths by the *M/lws* opsin was at 545–553 nm. Although many bats resemble diurnal mammals in having the potential for dichromatic vision, with both genes being intact, *Sws-1* was pseudogenised in all the rhinolophid and hipposiderid bats studied and in some pteropodids, especially cave-roosting taxa. Immunohistochemistry suggests that

the primary visual cortex may not respond to stimulation by UV light in these taxa (Xuan et al. 2012a), and behavioural responses to UV were also lacking (Xuan et al. 2012b). The lesser Asiatic yellow bat *Scotophilus kuhlii* and Leschenault's rousette *Rousettus leschenaultii* showed behavioural (Xuan et al. 2012b) and immunohistochemical responses in the primary visual cortex (Xuan et al. 2012a) to UV light at 365 nm. Two phyllostomid species (Pallas's long-tongued bat *Glossophaga soricina* and Seba's short-tailed bat *Carollia perspicillata*) possess significant cone populations and express opsins that are sensitive to short and long wavelengths. The short-wavelength opsin is sensitive to UV and may be advantageous for the detections of UV-reflecting flowers (Winter et al. 2003; Müller et al. 2009). Other bat species with intact *Sws1* genes may be UV sensitive, as ancestral reconstructions suggest UV sensitivity, with maximal sensitivity close to 360 nm (Zhao et al. 2009b).

Whether differences in UV sensitivity among bat taxa affect how species with intact and pseudogenised *Sws1* genes respond to different types of lighting remains unknown. Nevertheless the findings are of interest given that the wavelengths of maximum absorbance in bat opsins lie close to some of the peak emissions of wavelengths in a range of light types (Davies et al. 2013). Moreover emerging LED lighting technologies do not emit UV wavelengths, whereas older technologies, especially HPMV lamps, emit wavelengths that extend into the UV range and so HPMV lights may have been particularly conspicuous to horseshoe bats.

7.7 Observational Studies on Bats at Street Lights

Bats have been observed foraging around lights ever since artificial lighting became pervasive (Shields and Bildstein 1979; Belwood and Fullard 1984; Barak and Yom-Tov 1989; Acharya and Fenton 1999). Artificial light attracts many positively phototactic insects (Rydell 1992; Eisenbeis 2006), and most insectivorous bats are probably opportunistic feeders. Thus, they quickly identify and exploit insect accumulations such as swarming termites (Gould 1978) and insect clusters at artificial lights (Fenton and Morris 1976; Bell 1980; de Jong and Ahlén 1991). So some insectivorous bats probably profit from street lights because resource predictability and high insect densities increase foraging efficiency (Rydell 1992, 2006). For instance, 18 of 25 Neotropical insectivorous bat species which could be detected by acoustic monitoring were observed foraging around street lights in a small settlement. While more species were recorded in mature forest, total bat activity was lowest in forest but highest around street lights (Jung and Kalko 2010).

Bats prey on relatively large insects at street lights, mostly moths (Fenton and Morris 1976; Belwood and Fullard 1984; Acharya and Fenton 1992; Acharya 1995; Hickey et al. 1996; Acharya and Fenton 1999; Jacobs 1999; Pavey 1999; Fullard 2001). While moths are the most numerous insects around artificial lights (Huemer et al. 2010; Eisenbeis and Eick 2011), their contribution to a bat's diet can be much higher than expected from their relative abundance at street lights

(Belwood and Fullard 1984). This implies that bats focus on larger moths rather than smaller prey at street lights. Although moths were only captured in 36 % of attacks, northern bats *Eptesicus nilssonii* probably gain more than twice as much energy when feeding on moths at street lights than smaller dipterans in woodlands (Rydell 1992).

Aggregations of large insects around lamps enable bats to reduce foraging time and hence energy costs while maximising energy returns (Acharya and Fenton 1999; Jung and Kalko 2010). Big brown bats *Eptesicus fuscus*, for instance, spend less than half as much time outside the roost where in habitats where they forage at street lights than where they do not use lamps for hunting (Geggie and Fenton 1985). Hence, foraging at lights might be beneficial when a high foraging efficiency compensates for the potentially higher predation risk.

Bat activity and foraging efficiency at street lights are mainly determined by the number and size of prey insects available, both of which are strongly affected by the spectral characteristics of the light (Blake et al. 1994). Thus, the type of light indirectly influences bat activity. The light's attractiveness for insects increases with its UV spectral content. Aerial-hunting long-legged myotis *Myotis volans* and California myotis *M. californicus* consistently preyed on insects clustered in the cone of experimental black (UV) lights in North America (Bell 1980). While black light is not used for street lighting, similar results are seen with street lights that produce UV emissions. Thus, bat density can be an order of magnitude higher in towns illuminated by HPMV compared with those illuminated by HPS lights and road sections illuminated by HPMV rather than deep-orange LPS lights (Rydell 1992). In Britain, mean bat activity, likely to be mainly common pipistrelles *Pipistrellus pipistrellus*, is usually equal to or lower along roads lit by LPS lights than in dark sections, whereas bat activity is higher under HPMV than LPS lights or sections with no light (Fig. 7.3; Blake et al. 1994).

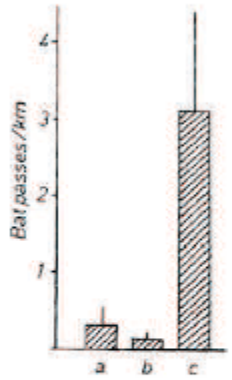

Fig. 7.3 Bat activity varies according to the type of artificial lighting. Activity of pipistrelle *Pipistrellus* spp. bats (mean and SD) along a 28 km stretch of road near Aberdeen, Scotland. *a* rural sections of the road without streetlamps, *b* village sections with sodium (*orange*) lamps and *c* a village with high-pressure mercury vapour lamps. From Rydell and Racey (1995)

7.8 Experimental Studies on Bats at Street Lights

Drawing conclusions from observational studies can be difficult, especially since confounding factors other than the presence of street lights can affect bat activity. Experimental field studies have demonstrated species-specific impacts of street lighting. Two 70 W HPS (DW Windsor Ltd, UK) lights, spaced and orientated to replicate street lights, were installed along preferred commuting routes of lesser horseshoe bats *Rhinolophus hipposideros*. The commuting activity of *R. hipposideros* (Fig. 7.4) and *Myotis* spp. was significantly reduced, and the onset of commuting delayed, on lit nights (Stone et al. 2009; Stone 2011). The following year the experiment was repeated on the same routes using white LED lights (Monaro LED, DW Windsor Ltd), at low (3.6 lux), medium (6.6 lux) and high (49.8 lux) light intensities. Activity of both *R. hipposideros* and *Myotis* spp. was significantly reduced during all lit treatments, and for *R. hipposideros*, the effect size at 49.8 lux was the same as that under HPS illumination. So both HPS and LED light disturbance caused spatial avoidance of preferred commuting routes by *R. hipposideros* and *Myotis* spp. (Stone et al. 2009), with no evidence of short-term habituation. Further work is needed to test for long-term habituation. In contrast, there was no significant change in bat activity under HPS and LED light treatments for *P. pipistrellus*, and for bats in the genera *Eptesicus* and *Nyctalus* (Fig. 7.5).

R. hipposideros and many other slow-flying species rely on linear habitat features for shelter from wind, rain and predators; acoustic orientation; and foraging

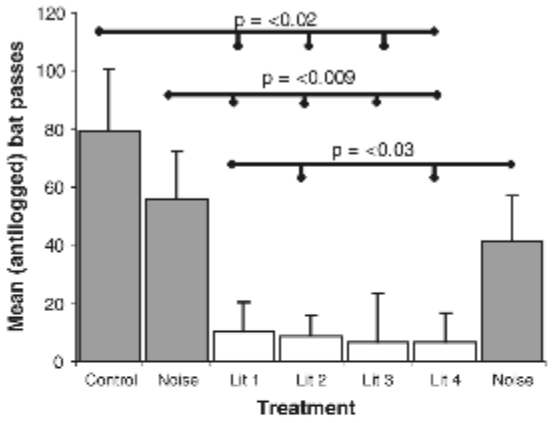

Fig. 7.4 Light-averse bat species show reduced activity along commuting routes subjected to high-pressure sodium (HPS) lighting. Activity of lesser horseshoe bats *Rhinolophus hipposideros* (mean passes and SE) in relation to lighting treatment. Significant within-subject differences with *p* values are shown. Treatments were control nights (no lighting treatment or generator), noise controls (HPS light units installed but switched off, generator running at night), 4 nights where lighting was switched on and powered by the generator (Lit 1 to Lit 4) and a final noise control. From Stone et al. (2009)

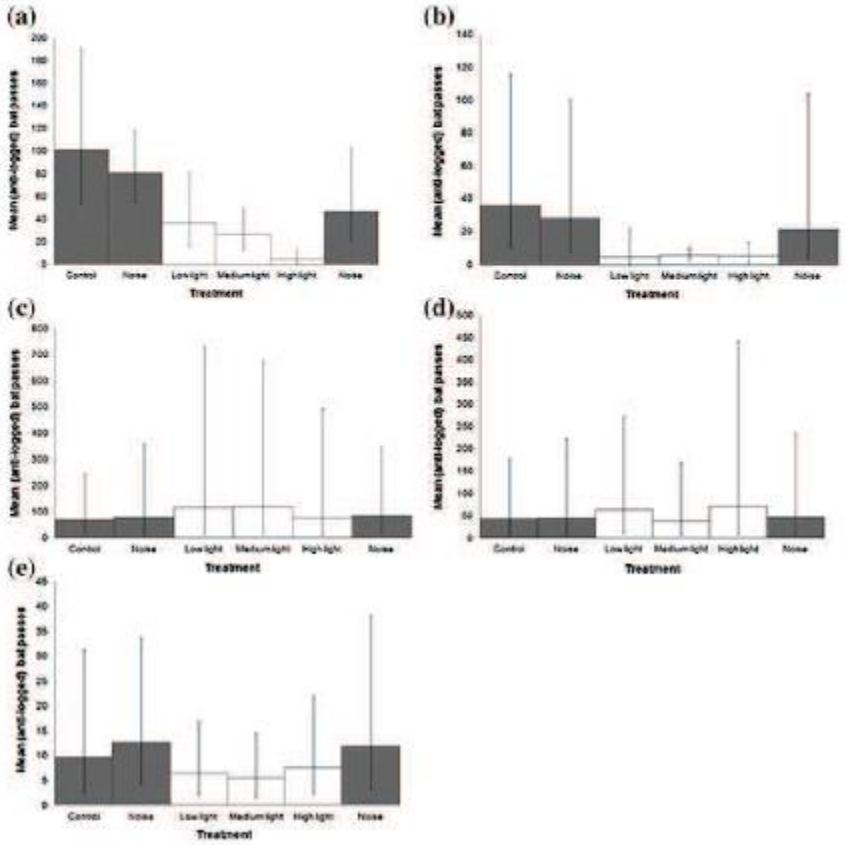

Fig. 7.5 Bats respond in different ways to LED lighting. Although the light-averse *Rhinolophus hipposideros* showed higher activity under more dimmed treatments compared with less dimmed ones, activity was still less than under unlit conditions. *Myotis* spp. showed negligible activity under all dimmed treatments. Geometric mean and confidence limits for bat passes along treatment hedges subjected to LED illumination at different light intensities are illustrated. Treatments were control nights (no lighting treatment or generator), noise controls (LED light units installed but switched off, generator running at night), 3 nights where illumination levels were modified (low light mean = 3.6 lux; medium light mean = 6.6 lux; and high light mean = 49.8 lux), and a final noise control. Bat passes were monitored on Anabat bat detectors and are shown for **a** *Rhinolophus hipposideros*, **b** *Myotis* spp., **c** common pipistrelle *Pipistrellus pipistrellus*, **d** soprano pipistrelle *Pipistrellus pygmaeus* and **e** *Nyctalus/Eptesicus*. From Stone et al. (2012)

(Verboom and Spoelstra 1999; Verboom et al. 1999). Using suboptimal routes with reduced cover to avoid artificial lighting may increase vulnerability to aerial predators and energetic costs due to increased exposure to wind and rain. So bats may have to travel further to reach foraging areas, reducing foraging time and increasing energetic losses, with consequential negative effects on reproduction rates and fitness. For example, juvenile growth rates were suppressed in the grey bat

Myotis grisescens with increased travel distance to foraging grounds (Tuttle 1976). Compensating for energetic losses by increasing foraging time may not be possible if, for instance, emergence and/or commuting is delayed by light pollution (Stone et al. 2009). Such delays also increase the risk that bats will miss the dusk peak in insect abundance, reducing the quality of foraging time. Delayed emergence could therefore affect the fitness of both individuals and the roost as whole.

Light disturbance along the commuting routes may isolate bats from their foraging grounds if the energetic costs of using alternative routes exceed the benefits. The commuting costs for *P. pipistrellus* become prohibitive when foraging areas are more than 5 km from the roost (Speakman 1991). Since bats select roosts based on the quality of surrounding habitat features, including linear connectivity (Jenkins et al. 1998; Oakeley and Jones 1998), maintaining optimal commuting routes is paramount. Whether fitness, or likely proxies of fitness, is affected by lighting needs further evaluation.

7.9 Winners and Losers: Light-Tolerant and Light-Averse Bats

Bats show variable responses to light pollution. Insectivorous bats that hunt in open spaces above the canopy (open-space foragers) or along vegetation edges such as forest edges, tree lines or hedgerows (edge foragers) are the species most tolerant of artificial lighting. They have evolved traits advantageous for foraging in sparsely structured habitats (Norberg and Rayner 1987; Neuweiler 1989) and so are preadapted to foraging in urban habitats (Rydell 2006; Jung and Kalko 2010; Jung and Threlfall 2016). Open-space foragers, such as the noctule *Nyctalus noctula*, typically have long narrow wings with a high aspect ratio, often combined with a high wing loading (weight/wing area). They have to fly fast to remain airborne and so use high-intensity, low-frequency narrowband echolocation calls that facilitate long-range detection of insects (Norberg and Rayner 1987; Rydell 2006; Kalko et al. 2008). When foraging at street lights, open-space foragers typically fly above the lamps, diving into the light cone to catch insects (Jung and Kalko 2010).

Edge foragers generally use echolocation calls with a conspicuous narrowband component, but usually also include a frequency-modulated 'broadband' component during the search phase, which is advantageous for ranging when flying close to obstacles. They comprise relatively fast-flying species with above-average aspect ratio and wing loading (e.g. *P. pipistrellus*), and species with an average aspect ratio and wing loading (e.g. *E. nilssonii*). Edge foragers tend to be more manoeuvrable than open-space foragers (Norberg and Rayner 1987; Kalko et al. 2008), and some can even conduct circuits inside the light cone when hunting insects at street lights (Jung and Kalko 2010).

Though most edge foragers fly with agility and speed (Norberg and Rayner 1987), they differ in their degree of synanthropism. While Kuhl's pipistelle

Pipistrellus kuhlii is recorded almost exclusively at street lights in southern Switzerland, *P. pipistrellus* forage to a similar extent both at lights and at least 100 m from lights (Haffner and Stutz 1985). Even within a species, foraging activity at lamps can be highly variable depending on the quantity of insects available: Geggie and Fenton (1985) never observed *E. fuscus* foraging around street lights in an urban environment, whereas in rural habitats feeding activity was greater at lights than in areas without lights. In spring and autumn, when artificial lights attract numerous insects in Sweden, *E. nilssonii* activity is about 20-fold higher in towns with street lighting than in non-illuminated towns, forest and farmland (de Jong and Ahlén 1991; Rydell 1991), with the bats flying back and forth above the street lights, regularly diving to within 1 m of the ground to catch insects.

Although fast-flying species adapted to forage in open areas, particularly bats of the genera *Eptesicus*, *Nyctalus* and *Pipistrellus*, may benefit from the increased foraging opportunities provided at lamps that attract high densities of insects, Stone et al. (2009, 2012) found no significant increases in bat activity for these 'light-tolerant' species during lit treatments. This could be due to two factors. First, HPS lights are less attractive to insects than white lights because their spectral content has less UV (Blake et al. 1994); for example, HPS street lights attracted fewer insects than white lights in Germany (Eisenbeis and Eick 2011). Second, the experimental nature of the study may have affected the results, since bats may need time to find and recognise newly installed lights as an attractive foraging source.

Though a relatively high proportion of aerial insectivorous bats may forage in suburban habitats, bat activity and the number of bat species decrease significantly towards highly urbanised areas. This is probably because both roosts and appropriate insect habitats are lacking, and those insects which are present might not aggregate at street lamps because the pervasive artificial lighting in city centres causes a dilution effect, rendering the lights less attractive for bats (Gaisler et al. 1998; Avila-Flores and Fenton 2005; Frank 2006; Rydell 2006; Jung and Kalko 2011; Jung and Threlfall 2016). In Panama, 18 of 25 insectivorous bat species frequently foraged around street lamps in a settlement bordering mature forest; the reduced vegetation cover in town constrained strictly forest-dwelling species from hunting at lamps (Jung and Kalko 2010). Yet, even some closely related and ecologically similar species may differ in their tolerance of urban habitats, and their potential to adapt to anthropologically altered habitats is best viewed from a species-specific perspective.

As compared to open-space foragers, bats at the other end of the wing shape spectrum, such as many horseshoe bats (Rhinolophidae) with their low aspect ratio wings and a low wing loading, rarely forage near artificial lights (Rydell 2006; Stone et al. 2009, 2012). They are mostly forest-dwelling and their short broad wings facilitate the high manoeuvrability needed for hawking insects in a cluttered environment (Norberg and Rayner 1987). However, their morphology only allows slow flight speeds, which might render them more vulnerable to predators when flying in a sphere of light away from protective vegetation cover (Jones and Rydell 1994; Rydell et al. 1996). Most forest-dwelling bat species emerge from

their roosts relatively late in the evening, presumably to minimise predation risk from diurnal birds of prey (Jones and Rydell 1994) and so may be 'hard-wired' to be light-averse. Furthermore, slow-hawking bats use echolocation calls that are adapted for short-range prey detection among clutter (Norberg and Rayner 1987), and so these may not be suitable for orientation in semi-open habitats where most street lights are positioned.

Myotis spp. in Canada and Sweden and brown long-eared bats *Plecotus auritus* in Sweden were only recorded away from street lights (Furlonger et al. 1987; Rydell 1992). In Australia, the chocolate wattled bat *Chalinolobus morio* avoided parks when lights were switched on (Scanlon and Petit 2008). Despite having street-lit areas in their home range, they were never utilised by greater horseshoe bats *Rhinolophus ferrumequinum* (Jones and Morton 1992; Jones et al. 1995). Artificial light reduced the foraging activity of pond bats *Myotis dasycneme* over rivers in the Netherlands (Kuijper et al. 2008), and commuting activity of *R. hipposideros* and *Myotis* spp. was reduced under LED and HPS street lights (Stone et al. 2009, 2012). It is likely that the *Myotis* spp. in Stone et al.'s studies were Natterer's bats *Myotis nattereri* (Stone 2011). *M. nattereri* emerges from roosts relatively late (Jones and Rydell 1994), at median light levels (3.5 lux, Swift 1997), lower than those recorded for *R. hipposideros* (Stone et al. 2009). *M. nattereri* and *R. hipposideros* use different echolocation strategies (Parsons and Jones 2000) but have similar flight and foraging patterns. *M. nattereri* has broad wings, prefers foraging in woodlands and is slow-flying and manoeuvrable, often foraging close to vegetation to glean prey (Arlettaz 1996; Swift 1997). This suggests that light-dependent predation risk limits the ability of these bats to take advantage of illuminated areas. Nevertheless, one large-eared horseshoe bat *Rhinolophus philippinensis* was repeatedly observed traversing 200 m of open grassland to forage extensively around artificial lights in Australia. The same lights were also used by eastern horseshoe bats *Rhinolophus megaphyllus* (Pavey 1999).

Extinction risk is highest in bat species with low aspect ratios (Jones et al. 2003; Safi and Kerth 2004), which are the species that show aversion to artificial lighting. Thus, species that may suffer most from light pollution are likely to be already threatened taxa.

7.10 Effects of Light Pollution on Ecosystem Services Provided by Bats

The impacts of lighting go far beyond changing the physiology, behaviour and/or distribution of individual species. Since congeners interact with each other as well as their prey and predators, light pollution is likely to have far-reaching consequences for the entire biome and the ecosystem services that bats provide. Insectivorous bats, for instance, significantly reduce the number of insects that cause damage to flora and fauna (Ghanem and Voigt 2012). The value of

insectivorous bats to the US agricultural industry by reducing insect populations was estimated to be $23 billion/year (Boyles et al. 2011).

Most studies to date have been on temperate-zone insectivorous bats. However, many tropical bats feed on nectar and fruits, thereby pollinating flowers and dispersing seeds of several hundred species of plants (Ghanem and Voigt 2012). Consequently, frugivorous bats are key for succession and maintaining plant diversity, especially in fragmented Neotropical landscapes (Medellin and Gaona 1999; Muscarella and Fleming 2007). However, very little is known about the impact of light pollution on this feeding guild. Southern long-nosed bats *Leptonycteris yerbabuenae*, a nectar- and fruit-eating species, used areas of relatively low light intensity when commuting (Lowery et al. 2009) and Oprea et al. (2009) rarely captured frugivorous bats along roads, although some were present in municipal parks. However, neither study could disentangle the influence of lighting from other factors related to urbanisation, such as altered vegetation cover or increased noise levels. Lewanzik and Voigt (2014) provided the first experimental evidence for light avoidance by frugivorous bats. They found that Sowell's short-tailed bat *Carollia sowelli*, a specialist on fruits of the genus *Piper*, harvested only about half as many fruits in a flight cage compartment lit by a sodium vapour street light than in a dark compartment, and free-ranging bats neglected ripe fruits that were experimentally illuminated (Fig. 7.6). Lewanzik and Voigt (2014) concluded that artificial light might reduce nocturnal dispersal of pioneer plant seeds. Since

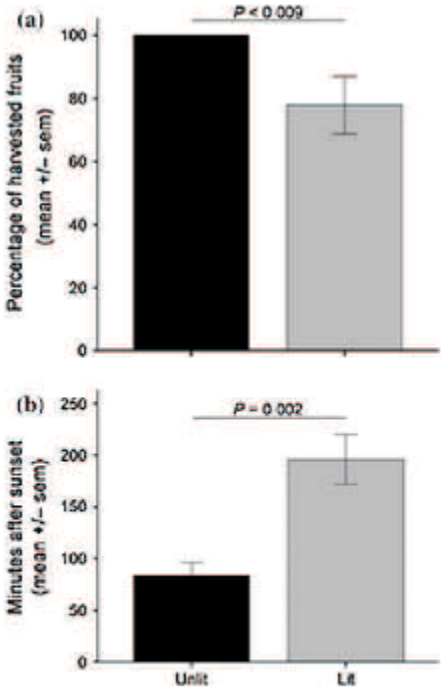

Fig. 7.6 Artificial lighting reduces and delays feeding behaviour on pepper plants by a frugivorous bat. **a** Percentage of harvested infructescences of *Piper sancti-felicis* among 14 marked plants harvested by Sowell's short-tailed bats *Carollia sowelli* in non-illuminated conditions (*black*) and under conditions where plants were illuminated by a street lamp (*grey*) in the field, **b** time after sunset when infructescences were harvested. From Lewanzik and Voigt (2014)

bat-mediated seed intake is particularly important during the early stages of succession (Medellin and Gaona 1999; Muscarella and Fleming 2007), light pollution might slow down the reforestation of cleared rainforests (Lewanzik and Voigt 2014).

7.11 Knowledge Gaps, Future Challenges and Mitigation Strategies

7.11.1 Knowledge Gaps

Light pollution has only recently been acknowledged as a threat to biodiversity (Hölker et al. 2010b), and there are still many unknowns about the interactions between bat species and artificial lighting sources (Hölker et al. 2010a). Most studies have focused on specific ecological behaviours such as foraging (Rydell 1992; Blake et al. 1994), predator–prey interactions, particularly with moths (Rydell et al. 1995; Svensson and Rydell 1998), commuting routes (Stone et al. 2009, 2012) and roost emergence (Downs et al. 2003). No long-term studies have been carried out to determine whether any of these behavioural changes have fitness consequences (Beier 2006; Stone et al. 2012). The only indication of potential population-level responses has been shown in Hungary on *Myotis* species, where juveniles roosting in illuminated buildings had a lower body mass than their counterparts in unlit roosts (Boldogh et al. 2007). However, this study did not establish whether a lower body mass in these juveniles reduced their survival rate after hibernation. It is particularly important to understand higher level responses for bat species because they have low fecundity rates, usually only producing one pup per year (Dietz et al. 2009), and so populations are sensitive to sudden changes (Stone et al. 2012).

Further studies are needed to address the impact of artificial lighting at the community level (Davies et al. 2012). The current literature highlights that artificial lighting causes species-specific responses (Rydell 1992; Stone et al. 2009, 2012; Jung and Kalko 2010), which could cause light-tolerant species to exclude light-averse species (Polak et al. 2011; Stone et al. 2012). Such competitive interactions have been proposed as the driving force behind changes in bat populations in Switzerland, where decreases in photosensitive *R. hipposideros* have been linked to increases in light-tolerant *P. pipistrellus* (Stutz and Haffner 1984; Arlettaz et al. 2000). It is believed that by avoiding street lights, *R. hipposideros* are foregoing profitable prey sources exploited by *P. pipistrellus* (Arlettaz et al. 1999, 2000).

So far research has focussed largely on insectivorous bats in temperate zones. Further research in tropical ecosystems is needed. For example, the forested areas of South-east Asia contain a high diversity and abundance of horseshoe bat species that are likely to be negatively affected by light pollution, and the impact of light

pollution on pollination and seed dispersal in the tropics and subtropics needs further investigation.

Research on the impacts of different light spectra in emerging technologies on bat activity and reproduction will be valuable; this is currently being investigated in the Netherlands as part of a large-scale investigation exposing a wide range of taxa to white, red and green LED lighting (see http://www.lichtopnatuur.org). With the current plans to switch to broader spectrum lighting sources, it is important to understand more about the spectral sensitivities of bats (Davies et al. 2012, 2013), especially given the recent findings on opsin genes highlighted above. Determining if there are spectral and intensity thresholds for different species would aid mitigation strategies and improve conservation initiatives (Stone et al. 2012; Gaston et al. 2013).

7.11.2 Mitigation Strategies

The most effective approach to reduce the detrimental effects of artificial lighting is to limit the growth of lighting by restricting unnecessary installations or removing them from areas already saturated with artificial lighting sources. This has the greatest potential to reduce light pollution and minimise ecological effects (Gaston et al. 2012). Turning off lights in areas commonly used by light-averse bats to forage, commute or roost during key times such as reproduction (Jones 2000) may be effective. Bats are faithful to maternity roosts due to the specific conditions they provide, and so conserving them is important for maintaining bat populations (Lewis 1995; Mann et al. 2002). However, some photosensitive bats may be disrupted even if areas were only lit for a short period of time (Boldogh et al. 2007), and switching off lighting may be challenged if it is perceived to jeopardise public safety (Lyytimäki and Rinne 2013).

Reducing the duration of illumination through part-night lighting (PNL) schemes could also help limit the adverse effects of light on nocturnal animals (Gaston et al. 2012). This has already been adopted by a number of local authorities in the UK, which switch off lights in specified areas between midnight and 05.30 to reduce CO_2 emissions and save money (Lockwood 2011). Since April 2009, lights along sections of motorways have also been switched off between these hours (Royal Commission on Environmental Pollution 2009). While this may help to reduce light pollution, it is unlikely to have significant ecological benefits since the lights remain switched on in the early part of the night, when bats and other nocturnal species undertake key activities such as foraging and commuting (Gaston et al. 2012). Intelligent lighting schemes, such as the use of motion sensors, have already been implemented in Portugal and may have more ecological benefits. The lights remain switched off unless needed and so still provide all the perceived public safety benefits (Royal Commission on Environmental Pollution 2009). However, these fluctuations in lighting levels may also be damaging to bats (Longcore and Rich 2004).

It is also important to reduce the trespass of artificial lighting to minimise the impact on bats. Newer technologies such as LEDs produce more directional light (Gaston et al. 2012), preventing the horizontal or upward emissions which contribute most to light pollution (Falchi et al. 2011). Effective luminaire design, installation of shielding fixtures and correct column height can also help focus light and avoid wasteful emissions (Royal Commission on Environmental Pollution 2009). In Lombardia, Italy, for example, 75 % of light pollution was due to poorly designed luminaires; the other 25 % was unavoidable reflection from road surfaces (Falchi 2011). Vegetation canopies such as hedgerows can also help decrease light trespass, which is crucial for many bat species that use linear features as commuting routes (Rydell 1992; Fure 2006). Diminishing trespass could create dark refuges, providing corridors for bats to forage in fragmented habitats (Longcore and Rich 2004; Stone et al. 2012; Gaston et al. 2012).

Light intensity has a significant effect on bat activity (Stone et al. 2012) and delays roost emergence (Downs et al. 2003). If bats delay foraging, they risk missing the peak abundance in insects that occurs shortly after dusk, so may not meet their energy requirements, which in turn could reduce fitness (Jones and Rydell 1994; Stone et al. 2012). In addition to implementing PNL, many local authorities are also dimming lights in specified areas (Gaston et al. 2012). This relies on local authorities already having lights such as LEDs that have the necessary centralised management system (International Energy Agency 2006). These schemes are more environmentally friendly and cost-effective (Gaston et al. 2012). However, dimming lights may not be beneficial to all bat species; Daubenton's bats *Myotis daubentonii*, for instance, only emerge from their roosts at very low light levels (less than 1 lux) (Fure 2006) and *R. hipposideros* and *Myotis* spp. avoid commuting routes illuminated to 3.6 lux (Stone et al. 2012). Since illumination levels of street lights are usually between 10 and 60 lux (Gaston et al. 2012), it may not be feasible to dim lighting to such low intensities without compromising public perceptions of safety (Stone et al. 2012; Lyytimäki and Rinne 2013).

7.11.3 Future Challenges

With a number of changes to street lighting planned in the coming years, including dimming, PNL and modifications to luminaire design to reduce light pollution, energy expenditure and greenhouse gas emissions, nightscapes could increase in heterogeneity, making it even more challenging to understand the impacts of artificial lighting on biodiversity (Gaston et al. 2012).

This is further complicated because current metrics for measuring emissions from light sources omit key biological information (Longcore and Rich 2004; Gaston et al. 2012). Illumination is measured in lux, which is defined as the brightness of a light according to human spectral sensitivities; spectral sensitivities of other taxa are often very different from ours (Peitsch et al. 1992; Briscoe and Chittka 2001). In bats, for example, many species can detect wavelengths in

the UV range (Winter et al. 2003; Wang et al. 2004; Müller et al. 2009). So HPS and LPS lamps could have the same intensity of light, e.g. 50 lux, but HPS lamps emit UV wavelengths, whereas LPS lamps do not, thereby affecting both bats and their insect prey in different ways (Longcore and Rich 2004). Since lux is commonly used as a metric by lighting engineers, designers and environmental regulators, migrating from this measure may thwart interdisciplinary communication (Longcore and Rich 2004).

Another challenge is to find more effective ways of quantifying the impact of artificial lighting on bat species. Current methods use acoustic survey methods to quantify bat activity; this underestimates the activity of bats that use low-intensity echolocation calls (O'Farrell and Gannon 1999). Crucially, we also need to determine whether artificial lighting has fitness consequences (Stone et al. 2012). A decrease in bat activity may have no relevance for fitness if, for example, the bats are able to utilise equally suitable alternative sites nearby.

A transdisciplinary approach needs to be adopted to minimise the impact of light on biodiversity, reduce CO_2 emissions, increase energy efficiency and reduce costs (Hölker et al. 2010a; Gaston et al. 2012). Scientists, policymakers and engineers need to work together to implement successful strategies (Stone et al. 2012). Moreover, it is vital to find ways to broaden awareness of light pollution and its ecological impacts. Since the public plays an integral part in agreeing mitigation schemes such as dimming lights, their support is pivotal in moving forward (Hölker et al. 2010a).

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Appendix II

PLOS ONE

RESEARCH ARTICLE

The Switch from Low-Pressure Sodium to Light Emitting Diodes Does Not Affect Bat Activity at Street Lights

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Abstract

We used a before-after-control-impact paired design to examine the effects of a switch from low-pressure sodium (LPS) to light emitting diode (LED) street lights on bat activity at twelve sites across southern England. LED lights produce broad spectrum 'white' light compared to LPS street lights that emit narrow spectrum, orange light. These spectral differences could influence the abundance of insects at street lights and thereby the activity of the bats that prey on them. Most of the bats flying around the LPS lights were aerial-hawking species, and the species composition of bats remained the same after the switch-over to LED. We found that the switch-over from LPS to LED street lights did not affect the activity (number of bat passes), or the proportion of passes containing feeding buzzes, of those bat species typically found in close proximity to street lights in suburban environments in Britain. This is encouraging from a conservation perspective as many existing street lights are being, or have been, switched to LED before the ecological consequences have been assessed. However, lighting of all spectra studied to date generally has a negative impact on several slow-flying bat species, and LED lights are rarely frequented by these 'light-intolerant' bat species.

Introduction

Increased use of artificial lighting over the last century has resulted in extensive changes in the nocturnal landscape [1,2]. Although artificial lighting benefits people [3,4], light pollution is widespread [5,6] and can affect organisms across a range of spatial scales [7].

Street lights are widely used around the world and have the potential for far-reaching effects on the environment, biodiversity and human health [8,9]. During the first part of the 21st century, the number of street lights in the UK continued to increase by 3% per annum [5] and their spectral signatures, i.e. the range of wavelengths that the lights emit, have changed [10,11]. There is currently a shift in street lighting from narrow light spectrum sources such as orange low-pressure sodium (LPS) and yellow high pressure sodium (HPS) lights to broad spectrum "white" lighting technologies such as light emitting diodes (LEDs) [9,12,13] (Fig 1).

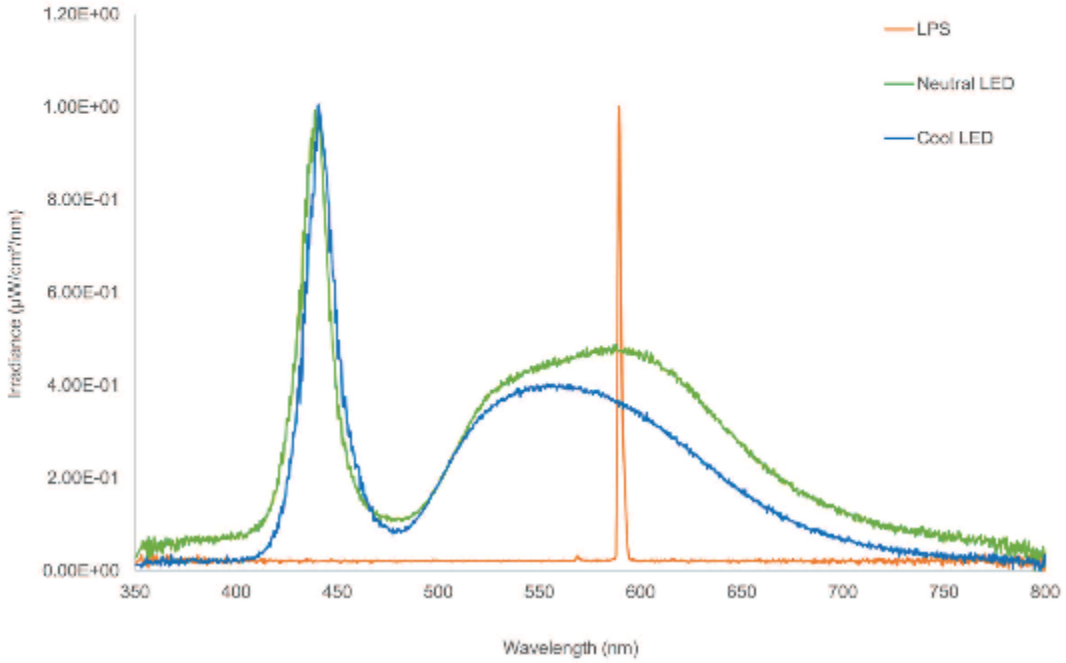

Fig 1. The spectral output of LPS and LED street lights, representative of the lights used in this study. LPS and neutral LED spectral outputs were taken from site J and the cool LED spectral output from site G, shown in Fig 2.

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There are three types of LED lights, cool, neutral and warm, that vary according to their correlated colour temperature (Kelvins). Cool LEDs appear 'cold' and have a high colour temperature (~6000 K), warm LEDs have a 'warmer' appearance (~2700 K), and neutral LED lights have a colour temperature between cool and warm LED lights (~4000 K) [14]. LED lights have a number of advantages, including increased energy efficiency, directionality, controllability (ability to dim and switch-off when not in use), longevity and flexibility of colour choice [9,13,14]. LED lights also have a higher colour rendering index (CRI), which expresses the capacity for a light source to yield the "true" colour of an object in relation to human vision [14]. Street lights exist primarily for perceived human safety benefits, and improved colour rendering for human vision enables people to see their surroundings more clearly, making them feel less vulnerable at night [15].

While these changes in spectral output accommodate human vision, many organisms have different spectral sensitivities [16]. Insects, for instance, are attracted to shorter wavelengths, particularly near the UV part of the spectrum, as this corresponds with the peak spectral sensitivities of their eyes [17–19]. Hence insects are common around old technology gas discharge street lamps that contain a high proportion of short wavelengths, such as high pressure mercury vapour (HPMV) lights [18]. However insects are rarer around LPS lights, which are essentially a monochromatic light source [20].

Bats are a valuable taxon for understanding some of the ecological impacts of artificial light since they exhibit species-specific responses to lighting, some bat species feed on insects attracted to street lights, whereas others avoid light [21,22]. Street lights attract fast-flying bats such as those in the genera *Eptesicus*, *Lasiurus*, *Nyctalus* and *Pipistrellus*, most probably because they prey on the insects attracted to the street lights [23–25]. These bats share a number of traits including aerial hawking [26], foraging in open habitats [27] and emerging relatively early after sunset, which is believed to coincide with peak insect availability [26]. *Eptesicus* and *Nyctalus* species tend to fly above street lights, diving near the light cone to feed, whereas *Pipistrellus* species hunt in and out of the light cone [12,28]. *P. pipistrellus* bats spend the majority of their time in dim or dark areas [29,30], so are only likely to use lights if the benefits associated with increased foraging success outweigh the perceived risk of predation [25]. In contrast, slow-flying bats such as *Myotis*, *Plecotus* and *Rhinolophus* species do not appear to be attracted to artificial lights [21,25,31]; these species rarely feed around street lights, possibly because the perceived risk of predation may be too high [26,32]. If artificial lights dominate the landscape, it may greatly reduce the high quality habitat available to these slow-flying species. A major concern is that the spread of artificial lights will have long-term effects on these slow-flying, light-intolerant bats.

Many local authorities across Britain are in the process of switching their old LPS and HPS lights to LED lights. One of the main drivers is cost, as local authorities can save money from reduced energy use and maintenance costs. Similar changes are happening across continental Europe and elsewhere in the world. However, LED lights are spectrally different from either LPS or HPS lights, the predominant street lights in the UK and around the world [33]. Species have existed under the yellow and orange hues emitted by sodium street light for decades; how bat activity will change following the introduction of modern broad spectrum lights is unclear [22]. The effect of an artificial light on each organism will depend on its photoreceptors, the spectral output of the light source, the intensity of the light and reflectance from the surrounding environment [9]. With that in mind we investigated how the switch-over from LPS to LED street lights affected bat activity and feeding behaviour.

Methods

Ethics Statement

All the data were collected remotely and there was no animal handling or manipulation. The study was reviewed and approved by the University of Bristol Ethics Committee approval number UB/14/031.

Site description and experimental set-up

A before-after-control-impact paired design (BACIP) [34], based on a previous study [35], was used to examine the effects of a switch from LPS to LED street lights at twelve sites in four counties (East Sussex, Gloucestershire, Hampshire and Hertfordshire) across southern England (Fig 2). A BACIP identifies if the impact being tested affects the system in question as it controls for variables such as environmental factors and seasonal changes [36], and so it was essential that the control and experimental lighting columns were matched as closely as possible. We used existing street lights and so site choice was governed by where local authorities were switching from LPS to LED street lights. Each site consisted of a pair of lighting columns (street lights), one control (remaining LPS throughout the study) and one experimental (changing from LPS to LED). Control columns were restricted to areas where LPS lights remained the dominant street lights throughout the study, whereas experimental columns were restricted to areas where LPS lights were the dominant lighting type before switch-over and LED lighting

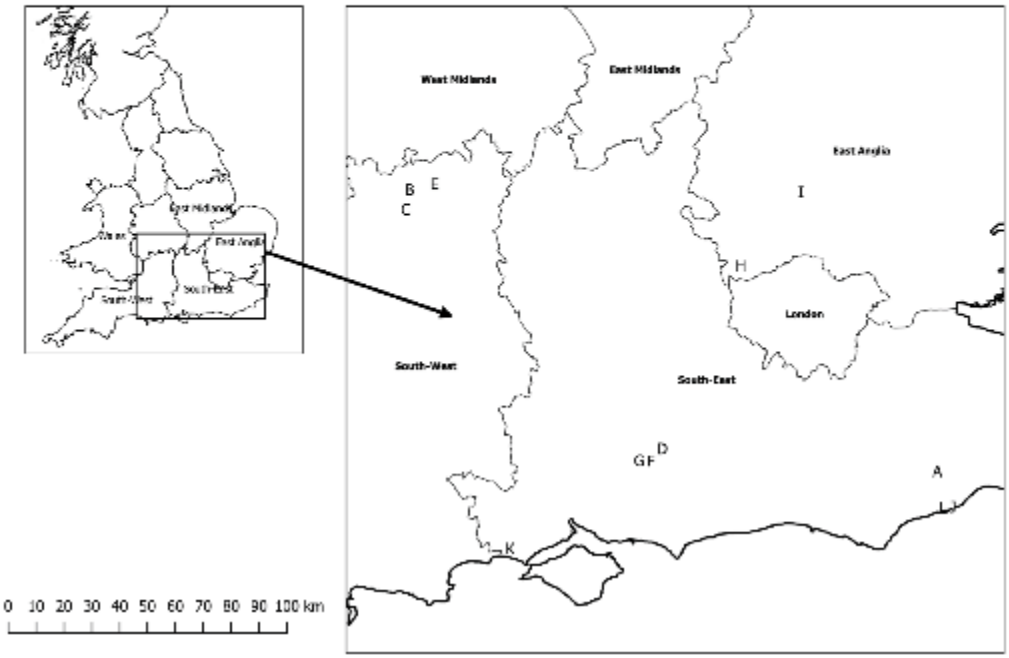

Fig 2. Locations of the 12 study sites in southern England. There were two lighting columns (street lights) at each site, one control, the other experimental.

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after switch-over. Paired columns were separated by a mean distance of 1.4 km (s.d. ± 0.9 km) to reduce the chance of recording the same bats around the control and experimental lighting columns. Sites were separated by a minimum distance of 1.86 km to ensure the samples were independent.

The sites were in suburban areas close to bat commuting and foraging habitats [37]; ten sites were in residential areas, the other two (sites H and I) were on A-class roads. Aerial imagery on Google Earth was used to match the distance to wooded areas, freshwater and grassland as closely as possible between the control and experimental columns (Table 1), although some variation was inevitable because this was a "real-life" experimental set-up. However, all sites were no greater than 154 m from a wooded area, defined as a stand of >10 continuous trees (mean 54.0 m, s.d. ± 32.3 m), 709 m from a freshwater source (mean 320.0 m, s.d. ± 182.2 m) and 428 m from grassland with an area >0.6 ha (mean 110.9 m, s.d. ± 110.1 m). Within sites, there was a mean difference between the control and experimental columns of 35.4 m (s.d. ± 32.5 m) between distance to a wooded area, 130.4 m (s.d. ± 144.5 m) to a freshwater source and 63.0 m (s.d. ± 50.7 m) to grassland.

While there was variation between sites, control and experimental columns in each pair were matched for height (m), output (watts) and illuminance (lux). The local authorities provided information on the light type, output and column height. Within sites, the column heights, light type and output were identical between the control and experimental columns

Table 1. Specifications of the LPS and LED street lights used in this study. Control and experimental lighting columns in each pair were matched in terms of height (m) and output (watts) prior to switch-over. For the experimental columns, the output and illuminance readings of the LED lights after switch-over are shown in brackets. Proximity to key habitats is shown for each column. Letters denote the 12 study sites; the location of each site is shown in Fig 2. Power (watts) can reduce, but illuminance (lux) can stay the same or increase after the switch-over to LED lights. This is because LED lights are more energy efficient and the lanterns are more directional than LPS lights.

Site	Column	Column height (m)	Power (watts)	Illuminance (lux)	Distance to a wooded area (m)	Distance to freshwater (m)	Distance to grassland (m)
A	Control	6	55	41	22	71	339
A	Experimental	5	35 (14)	28 (26)	56	258	161
B	Control	5	55	28	45	515	51
B	Experimental	5	55 (18)	31 (71)	81	465	28
C	Control	5	35	3	55	55	67
C	Experimental	5	35 (27)	3 (57)	78	413	25
D	Control	5	26	8	60	390	131
D	Experimental	5	26 (10)	3 (20)	52	333	46
E	Control	5	35	38	36	29	84
E	Experimental	5	35 (27)	31 (60)	154	161	9
F	Control	5	26	28	46	53	58
F	Experimental	5	26 (10)	41 (20)	54	90	135
G	Control	5	26	2	91	59	30
G	Experimental	5	26 (10)	3 (19)	91	59	82
H	Control	10	91	60	87	215	17
H	Experimental	10	91 (107)	60 (109)	17	397	16
I	Control	10	91	118	7	14	55
I	Experimental	10	91 (107)	114 (178)	59	68	2
J	Control	5	35	29	31	206	127
J	Experimental	5	35 (14)	40 (29)	4	175	177
K	Control	5	26	2	50	252	163
K	Experimental	5	26 (10)	28 (18)	33	709	156
L	Control	5	35	41	36	137	295
L	Experimental	5	35 (14)	40 (25)	50	157	428

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except for site A, where the control column was 6 m in height and had an output of 55 watts, whereas the experimental column was 5 m in height and had an output of 35 watts (Table 1). A combination of neutral and cool LED lights (4000–5700K) was used. Light measurements from control and experimental lighting columns were taken with a lux meter (photometric system) and a spectrometer (radiometric system) to ensure that the light output and intensity of the paired street lights were comparable. Illuminance was measured with a TES 1330 lux meter (ATP Instrumentation Ltd, Leicestershire, UK) held horizontally 1.8 m from the ground directly beneath the street light. Irradiance (absolute intensity of the street light) was measured ($\mu W/cm^2/nm$) 4 m directly below the lantern with a tripod and using a calibrated Ocean Optics USB 2000 spectrometer, a P200-5-UV/VIS patch cord and a CC-3 cosine corrector. A Gershun tube was used to reduce the acceptance angle (the amount of light that falls on the sensor) to ensure that the irradiance measurement was from the street light. Ensuring all light readings were taken 4 m from the lantern enabled absolute intensities to be compared between columns of varying heights. Since environmental variables such as temperature, precipitation and cloud cover affect light readings [38], we took light measurements on clear dry nights when there was no full moon.

Measuring and identifying bat calls

Field work took place between May and October 2014. Bat activity was measured using Song Meter SM3 Bat Recorders (Wildlife Acoustics Inc., Massachusetts, USA). Prior to deployment, all detectors were tested in a semi-anechoic chamber and the microphone placed 1 m and at an angle of 45° from the speaker of an ultrasound generator, which then played a series of high frequency sounds between 20 and 120 kHz. All detector systems used were comparable in sensitivity as determined by visual inspection of waveforms in BatSound (Pettersson Elektronik, Uppsala Science Park, Sweden). Four detectors were used to further minimise bias: they were randomised between sites, but the same detector was used before and after switch-over for both the control and experimental lighting columns.

Street sign and tamtorque sign fixing clamps were used to attach the bat detectors on average 1.09 m (range 0.73 m to 2.07 m) from the lantern to ensure a standardised method across lighting columns (S1 Fig). Recordings were made simultaneously at both the control and experimental columns for three consecutive nights before and after the switch-over. Bat detectors were set to record bat activity using triggers from thirty minutes before sunset on the first night until thirty minutes after sunrise on the fourth morning. The microphone on the detector was pointing in the same direction as the lantern. All detectors ran the same program, which was generated on SM3 Configurator 1.2.4 (Wildlife Acoustics Inc., 2015) and files were stored as waveform audio files (WAV). The settings on the detectors were: high pass filter 16 kHz; sample frequency 384 kHz; minimum frequency 16 kHz; maximum frequency 120 kHz; maximum recording time 15 seconds; and trigger level 12 dB. Detectors were removed between treatments and post switch-over recordings were made a minimum of seven days (mean 14.9 days, s.d. ± 5.3 days) after conversion to enable the bats to adjust to the new lights [35].

It is not possible to record individual bats using acoustical methods, so bat activity was monitored as the number of passes over the three recording nights. A bat pass was defined as when the time between pulse intervals was four times the interpulse interval [21,31,39]. We also investigated bat feeding behaviour around the control and experimental columns. Before catching an insect, a bat produces a feeding buzz, which is distinguishable from other echolocation calls by its higher repetition rate [32,40]. Relative feeding activity was measured using a 'buzz ratio', which is the proportion of call sequences that included feeding buzzes over the three recording nights [41]. Buzz ratio acted as a proxy for insect activity, the assumption being that the higher the buzz ratio, the more attractive the light source was to insects. We used buzz ratios as a measure of feeding relative to general activity at LPS and LED street lights.

We analysed the bat calls using the automatic identification software programme Kaleidoscope Pro (v0.1.1.20, Wildlife Acoustics Inc., Massachusetts, USA) with British Bat Classifiers (v1.0.5). All bat calls were also validated manually using Kaleidoscope viewer and Bat Sound with the parameter values stipulated in [42] to ensure correct identification. If there were any discrepancies between the manual and automatic methods of species identification, the manual identification was used. Manual validation was used to record multiple passes and/or species per file. Bats were identified to either species (*Eptesicus serotinus*, *Pipistrellus nathusii*, *P. pipistrellus* and *P. pygmaeus*) or species groups (*Myotis* spp., *Nyctalus* spp. and *Plecotus* spp.) depending on how diagnostic the calls of particular species were [43].

Data analysis

The pairings were an integral part of the experimental design as they accounted for any environmental and/or seasonal changes between the two recording periods. To determine if the switch-over from LPS to LED street lights affected bat activity, we were interested in the difference in the number of bat passes before and after the switch-over between the control and

experimental lighting columns [44]. If the LED lights did not affect bat activity, the difference between the control and experimental column in each pair would be negligible or inconsistent between pairs [45].

As the bat activity data were not normally distributed, we used a series of Wilcoxon signed rank tests to determine if there was a difference in the number of bat passes between LPS and LED street lights compared with differences in the paired control lights where no switch-over occurred. We compared bat activity of all species combined, and separately for *P. pipistrellus*, *P. pygmaeus* and *Nyctalus* spp., which together contributed 90% of all recorded bat calls. Similarly, buzz ratio data were not normally distributed and so a Wilcoxon signed rank test was used to test for differences between LPS and LED lighting columns. The buzz ratios of all species were compared, as were the data for *P. pipistrellus*, which contributed 80% of all buzz ratios recorded. Bonferroni corrections were used to adjust for multiple testing to reduce the risk of false positives; a significant difference between LPS and LED for the bat activity and buzz ratios was accepted if $p < 0.0125$ and $p < 0.025$ respectively [46]. Species richness and species diversity indices [47] were calculated to compare relative abundances of bat species around LPS and LED street lights; the diversity indices were based on the total number of bat passes for each species at control and experimental columns both before and after the switch to LED. All statistical and descriptive analyses were carried out in R Studio (version 0.99.451) [48]. The Wilcoxon signed rank test was conducted using the 'coin' package [49] and the species richness and species diversity indices were conducted using the 'vegan' package [50].

Results

Bat activity

There were 30,416 files from the 12 sites (24 columns). These contained 37,124 bat passes, an average of 1.2 passes per file: 70.0% of passes were *P. pipistrellus*, 13.0% *Nyctalus* spp., 9.4% *P. pygmaeus* and 7.7% *Myotis* spp. (electronic supplementary material, S1–S4 Tables). However, nearly all the *Myotis* spp. calls were recorded from site E after the experimental column had been switched to an LED light. *P. pipistrellus* were found at both control and experimental lighting columns across all sites, *P. pygmaeus* were found across all sites but only at ten of the twelve control columns, and *Nyctalus* spp. were recorded at all control lighting columns but only nine of the experimental columns.

There was no significant difference in the number of passes from all species before and after the switch-over to LED between the control and experimental columns ($W = 30$, $Z = -0.706$, $p = 0.4802$; Fig 3A). Bat activity was not significantly different between LPS and LED street lights for *P. pipistrellus* ($W = 30$, $Z = -0.706$, $p = 0.4808$; Fig 3B), *P. pygmaeus* ($W = 36.5$, $Z = -0.1963$, $p = 0.8444$; Fig 3C) or *Nyctalus* spp. ($W = 35.5$, $Z = -0.2751$, $p = 0.7832.8136$; Fig 3D). Thus the switch-over from LPS to LED street lights did not have a significant effect on either total bat activity or individual species/groups for which we had adequate data. In many cases the responses at the control and experimental lighting columns mirrored each other, i.e. when there was an increase in the number of bat passes at the control column, there was a similar increase at the experimental column and *vice versa*. Furthermore, the direction of change between the control and experimental sites was consistent across eleven of the twelve sites, although at sites E and I the magnitude of change at the experimental columns was greater than that at the control columns.

Buzz ratios

There was no significant difference in buzz ratios between the LPS and LED street lights for all bat species ($W = 53$, $Z = 1.0983 p = 0.2721$; Fig 4A) or for *P. pipistrellus* ($W = 46$, $Z = 0.5491$,

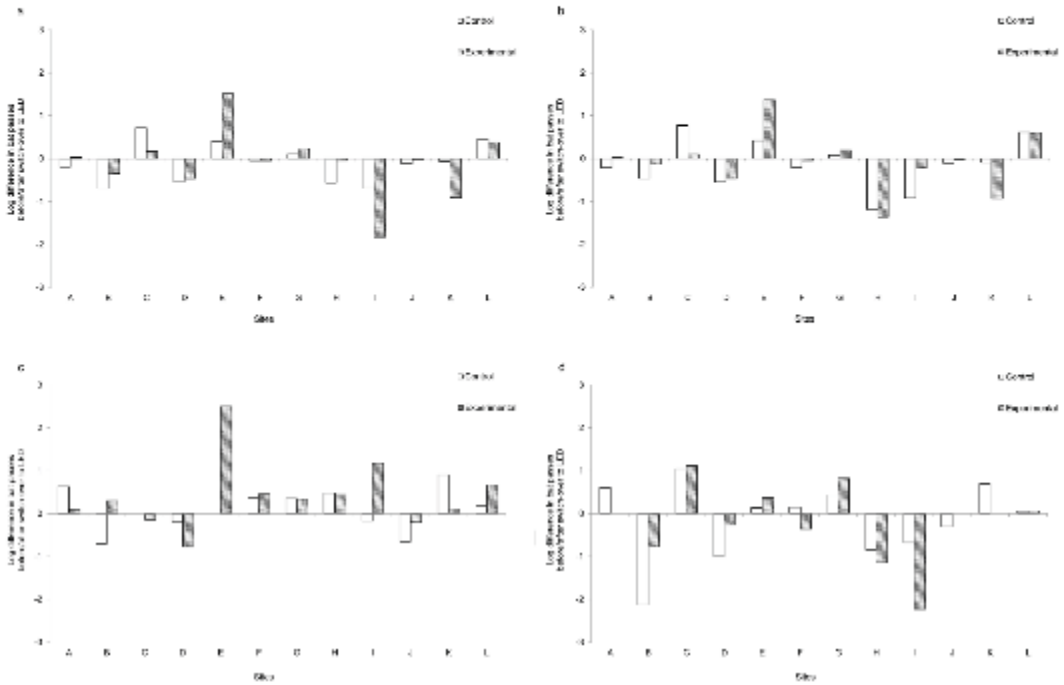

Fig 3. The differences in the log bat passes (number of bat passes after the switch-over minus the number of bat passes before the switch-over) for the control and experimental columns in each pair. A positive value indicates that there were more bat passes after the switch-over compared with before, and a negative value indicates more bat passes before compared with after the switch-over. (a) total bat activity, (b) *Pipistrellus pipistrellus*, (c) *Pipistrellus pygmaeus* and (d) *Nyctalus* spp. Letters denote the 12 study sites; the location of each site is shown in Fig 2.

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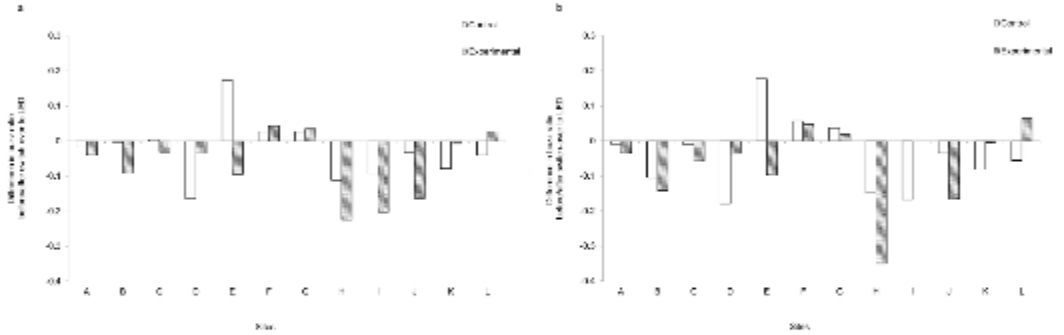

Fig 4. The difference in the buzz ratios (proportion of feeding buzzes after the switch-over minus the proportion of feeding buzzes before the switch-over) for both the control and experimental lighting columns. (a) all bat species and (b) *Pipistrellus pipistrellus*. Letters denote the 12 study sites; the location of each site is shown in Fig 2.

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Table 2. Species richness and Shannon-Wiener, Simpson's and Fisher's alpha diversity indices before and after switch-over from LPS to LED lights.

Sites	Species richness	Shannon-Wiener index	Simpson's index	Fisher's alpha index
Control -before	8	0.926	0.514	0.892
Control—after	8	0.677	0.351	0.839
Experimental—before	8	0.606	0.452	0.677
Experimental—after	7	0.906	0.496	0.891

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$p = 0.5829$; Fig 4B). As with the total number of bat passes, patterns of change at each site were usually the same at both the control and experimental columns. However, there was a marked difference at site b, where there was a decrease in the buzz ratio even though the number of bat passes at the experimental site increased by more than 32 times after the switch-over to a LED light (Fig 3A).

Species richness

Species richness and diversity indices showed that the same species were in the vicinity of the LPS and LED lights and diversities remained consistent across the control and experimental sites for the two time periods (Table 2), thus the proportion of calls per species varied little between recording periods or light type.

Discussion

The activity of all bats combined, and *Pipistrellus* and *Nyctalus* species, was not significantly different around LED and LPS street lights. While several studies have recorded fewer bats around LPS compared to 'white' street lights [23,24,25], the 'white' lights used in those studies were HPMV street lights that, unlike LED lights, emit UV light. Compared to other spectral emissions, UV light is attractive to many insects that bats prey on. Although LED lights contain more short wavelengths than LPS lights, it is likely that both light types are equally attractive to insects since neither contains UV light [24,26,35]. Moreover, we found that the buzz ratio did not change between the two types of street lights, again suggesting that LPS and LED lights had a similar effect on overall insect activity.

In addition to LED lights, there has been interest in the ecological impacts of other new lighting technologies such as metal halide lights. Both metal halide and LED lights are broad spectrum lights and so have a high colour rendering index [35] but, unlike LEDs, metal halide lights are a gas discharge lamp and emit a high proportion of short wavelengths, including some UV emissions [14]. Some local authorities are replacing LPS lights with metal halide rather than LED lights [51] to save money on installation costs. Unlike our study, activity of both *Nyctalus* and *Pipistrellus* species increased around metal halide compared with LPS lights in a BACIP experiment with fewer study sites [35]. However, while it was predicted that insect activity would be greater around the metal halide lights, the buzz ratio did not vary between the two light types, suggesting that the bats may be attracted to metal halide lights for some reason other than feeding. This may be related to the spectral sensitivities of bat eyes, as vesper bats can see UV light [52]. Alternatively, this may be due to the limitations of the AnaBat detectors (SD1 and AnaBat II; Titley Electronics, Ballina, New South Wales, Australia) used in that study [35]; these are less sensitive than the full spectrum Song Meter SM3 Bat Recorders we used and can fail to record the lower-amplitude parts of bat calls, such as feeding buzzes [12]. Since LED lights do not affect bat activity in any way that is different from LPS lights,

replacing LPS lights with LED rather than metal halide lights will cause less change to bat activity around street lights.

We recorded few bats from the genera *Myotis*, *Plecotus* and *Rhinolophus*, probably because they avoid light when commuting and foraging; HPS and LED street lights showed similar effect sizes on reducing the number of passes of *Rhinolophus hipposideros* bats [21]. The low intensity echolocation calls of *Plecotus auritus* [42], the commonest species of *Plecotus* in Britain, will also have contributed to the paucity of data for this genus. The low numbers of *Myotis*, *Plecotus* and *Rhinolophus* bats we recorded is also likely to be attributable in part to the location of the study sites. Street lights are mostly in built-up locations, and so we worked in suburban areas where there were suitable habitats for bats. However, these are generally more open, less cluttered habitats, where slow-flying species of *Myotis*, *Plecotus* and *Rhinolophus* are less likely to occur [26,53], although we recorded a three-fold increase in *Myotis* spp. activity at site B following switch-over. While artificial lighting generally has a negative effect on *Myotis* species [21,27], this increase at the experimental site may be related to nearby swarming behaviour, which takes place in autumn, and would explain why there was such a large increase in bat activity despite a reduction in the number of feeding buzzes. When UV lights were erected in a desert in the USA, the insects attracted to the lamps were preyed on by a number of bats, including species of *Myotis* [54,55]; this may be due to differences in spectral properties and intensities between the UV lamps and the LED light studied here that emitted no UV.

If buzz ratio is a good proxy for insect activity, our results suggest that there is no difference in the absolute, but not necessarily relative, abundance of the groups of insects eaten by the species of bat we recorded [56] around LPS and LED street lights. While there have been no direct comparisons of insect activity around LPS and LED lights, there have between HPS and LED lights, although HPS lights have broader spectral emissions than LPS lights. However, the findings are conflicting. A study in New Zealand found that neutral 4000 K LED lights attracted 48% more insects than HPS lights [22], whereas a study in Germany with a mixture of cool (6500 K) and warm/neutral LEDs (3000/4100 K) found that more insects were attracted to HPS lights [57]. These differences may reflect differences in local insect communities, the habitats in which the two studies were carried out and/or because neither study was broad-scale.

The ecological impacts of artificial lighting are complex. More work is needed on how both bats and their insect prey, and other taxa, respond to different street lights before we can properly assess the ecological impacts of new lighting technologies, particularly LEDs, as these will soon be used worldwide and so have the potential for far-reaching ecological effects [58]. Due to our experimental design, there was some variation between sites in the power of the different light sources (10–107 watts) and correlated colour temperature (4000–5700 K) of the LED street lights we used. We were unable to control for this because the study was carried out in a "real life" setting, and we had to use the lighting being installed by the local authority. However, we do not believe that colour temperature was a confounding variable because there is little difference in insect attraction between off-the-shelf LEDs with different colour temperatures (2700 K and 6000 K) [22]. To understand the effects of LED lighting on bats, and enable the results to be incorporated into lighting polices, it is important that future studies include all relevant information such as light source, output, spectral distribution, luminous flux and flicker rate [59], as well as data on habitat quality and environmental variables. It is also important that studies should involve multiple sites in different areas to avoid drawing conclusions based on local effects.

Conservation perspective

From a conservation viewpoint, our results are encouraging because they suggest that the large-scale replacements of old lighting technologies by LED lights currently taking place in many parts of the U.K, as well as in other countries [9], will not affect bat activity significantly differently from what currently occurs at LPS street lights. While there may be different impacts on other taxa, our data suggest that broad spectrum light sources such as LEDs will not necessarily have a greater ecological effect on bats than narrow spectrum lights [9].

However, it is important that these results are viewed alongside the wider impact of artificial lighting on bats. The majority of echolocation calls we recorded were from three species/groups of bats, which are typically considered as light-tolerant. There have been a number of studies showing the detrimental effects of lighting on roost emergence [60], commuting [31,61] and fitness [62] of a number of slow-flying bat species. Many of these are already vulnerable to habitat loss and urbanisation [63], and are further disadvantaged by the spread of artificial lighting.

Conclusions

LED lights are widely perceived as being environmentally friendly because of their lower CO_2 emissions. The results from this paired study also indicate that the switch-over from LPS to LED street lights did not affect the activity of bat species typically found in close proximity to street lights in suburban environments in the UK. The direction of change within a pair was consistent for eleven of the twelve sites and, as this experiment was carried out at a broad geographical scale, the switch-over from LPS to LED street lights is unlikely to have an effect on bat activity. From a conservation perspective this is a positive outcome as many existing street lights are being, or have already been, switched to LED in the UK and across the world. The lack of change in the number of feeding buzzes suggests that there was no significant change in the overall abundance around street lights of those insect groups eaten by bats, although more data are needed on individual insect groups, and how LEDs affect species interactions.

Supporting Information

S1 Fig. The arrangement of the SM3 bat detector and microphone on each of the lighting columns.
(TIF)

S1 Table. The number of passes and buzz ratios for total bat activity at the control and experimental lighting columns before and after the switch-over to LED lights. The buzz ratios are shown in brackets.
(DOCX)

S2 Table. The number of bat passes and buzz ratios for *Pipistrellus pipistrellus* at the control and experimental lighting columns before and after the switch-over to LED lights. The buzz ratios are shown in brackets.
(DOCX)

S3 Table. The number of bat passes for *Pipistrellus pygmaeus* at the control and experimental lighting columns before and after the switch-over to LED lights.
(DOCX)

S4 Table. The number of bat passes for *Nyctalus* spp. at the control and experimental lighting columns before and after the switch-over to LED lights.
(DOCX)

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Author Contributions

Conceived and designed the experiments: EGR SH GJ. Performed the experiments: EGR. Analyzed the data: EGR. Contributed reagents/materials/analysis tools: EGR GJ. Wrote the paper: EGR SH GJ. Supervised the study: SH GJ.

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Appendix III

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Research

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THE ROYAL SOCIETY PUBLISHING

Effects of dimming light-emitting diode street lights on light-opportunistic and light-averse bats in suburban habitats

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Emerging lighting technologies provide opportunities for reducing carbon footprints, and for biodiversity conservation. In addition to installing light-emitting diode street lights, many local authorities are also dimming street lights. This might benefit light-averse bat species by creating dark refuges for these bats to forage and commute in human-dominated habitats. We conducted a field experiment to determine how light intensity affects the activity of the light-opportunistic *Pipistrellus pipistrellus* and light-averse bats in the genus *Myotis*. We used four lighting levels controlled under a central management system at existing street lights in a suburban environment (0, 25, 50 and 100% of the original output). Higher light intensities (50 and 100% of original output) increased the activity of light-opportunistic species but reduced the activity of light-averse bats. Compared to the unlit treatment, the 25% lighting level did not significantly affect either *P. pipistrellus* or *Myotis* spp. Our results suggest that it is possible to achieve a light intensity that provides both economic and ecological benefits by providing sufficient light for human requirements while not deterring light-averse bats.

1. Introduction

Over the last 60 years, artificial light at night (ALAN) has increased globally on average by 6% per annum [1]. Although more prevalent in developed countries, ALAN is now considered a global threat because of increasing urbanization and industrialization in many developing countries [2,3]. ALAN is the result of a number of artificially lit sources, but street lights are one of the main contributors as they are installed in most towns and cities across the world [3,4].

Many local authorities across Britain are replacing old lighting stock such as low-pressure sodium (LPS) and high-pressure sodium (HPS) street lights with light-emitting diode (LED) street lights [5]. LED street lights offer a number of advantages over older lighting technologies, including increased energy efficiency, flexibility and longevity [6]. In Britain, LED lights are predicted to contribute up to 70% of the outdoor and residential lighting by 2020 [7]. As well as installing LED lights, many local authorities are implementing strategies to save money and reduce their carbon footprints, such as part-night lighting and dimming. It is relatively easy to employ dimming regimes with LED lights because they have a rapid on/off time [6,8]. Dimming levels can be implemented and adjusted remotely using a central management system (CMS) [3,9]. Dimming LED street lights is typically carried out by pulse-width modulation, which manipulates the duty cycle of a signal, so that the amount of 'on' time is reduced, but the spectral output of the light is unchanged [10,11].

Bats are a useful taxon to study the ecological impacts of light because they are nocturnal and their response to ALAN varies across species. A number of species are considered 'light opportunistic' as they feed on the large numbers of insects attracted to lights [12,13]: the attraction-by-insects hypothesis [14]. In Europe, these species are typically from the genera *Eptesicus*, *Nyctalus* and *Pipistrellus*. However, even light-opportunistic bats such as *Pipistrellus pipistrellus* will avoid lit areas when commuting in urban habitats, preferring to cross gaps in vegetation where there is little artificial light [15]. They also avoid lit areas when drinking at water sources [16].

Conversely, light-averse bats, such as those species from the genera *Myotis*, *Plecotus* and *Rhinolophus*, seem to be negatively affected by all types of street lighting. It is thought that because light-averse bats are often slower flying, more manoeuvrable species [17,18], they avoid light to reduce the risk of predation [19,20]. Many are also of conservation concern because their wing shape limits dispersal and movement [21], and hence they are particularly vulnerable to anthropogenic pressures such as urbanization and the associated ALAN. As dimming reduces both the light intensity of the street light and the amount of light distributed from the light source, it might create dark refuges that light-averse bats could use for commuting and foraging in urban areas [3].

There are many examples of artificial lighting affecting orientation, reproduction, communication and foraging in nocturnal taxa [22–26]. However, few studies have explored the biological impacts of varying light intensities. For example, the reproduction and survival of fruit flies, *Drosophila melanogaster*, are negatively affected by increased light intensity [27]. Increased light intensity also has a detrimental effect on the activity and melatonin level of great tits, *Parus major* [28] and activity patterns of blue tits, *Cyanistes caeruleus* [29], interrupts immune responses of Siberian hamsters, *Phodopus sungorus* [30], and Swiss Webster mice, *Mus musculus* [31], but does not affect sleep in *Parus major* [32].

Studies on the effects of light intensity on bat activity have highlighted that even low levels of ALAN have a detrimental effect on the activity of light-averse species [26,33]. Even when LED street lights were dimmed to a low level (mean 3.6 lux, range 2.90–4.86 lux), there were significantly fewer passes from the light-averse bats *Myotis* spp. and *Rhinolophus hipposideros* than on unlit nights [26]. However, dimming street lights to an intensity below 3.6 lux may not be feasible: street lights exist for human safety and if humans cannot see their surroundings clearly because the light intensity is too low, this nullifies the benefits of having street lights [26,34].

Our aim was to determine whether street light dimming regimes currently used by local authorities can have ecological benefits for bats as well as economic benefits. We tested the following two hypotheses:

(i) bat activity of the light-opportunistic bat *P. pipistrellus* will decrease at dimmed LED lights compared with undimmed LED lights owing to reduced insect abundance at dimmed street lights; and

(ii) bat activity of light-averse species from the genus *Myotis* will increase at dimmed LED lights compared with undimmed LED lights because the reduced light distribution will create dark refuges for light-averse bats to forage and commute.

2. Methods

2.1. Experimental design

Fieldwork took place between May and August 2015 at 21 sites using existing street lights in Hertfordshire, southeast England. Each site consisted of three lighting columns (lamp posts), which ran

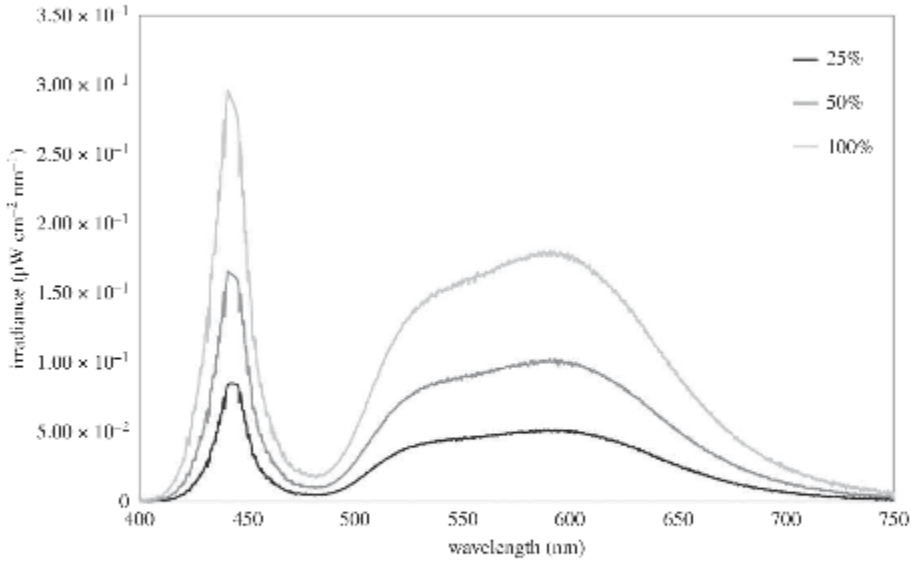

Figure 1. The spectral output of LED street lights at the three lighting levels (25%, 50% and 100%) from one of the 21 sites chosen at random.

a series of lighting levels: 0%, 25%, 50% and 100% of the original output. These lighting levels refer to changes in duty cycle as described in the Introduction. Illuminance values for the four lighting levels are provided in the Results. As our aim was to assess the impacts of different street lighting levels, we used three adjacent lighting columns per site to ensure that a stretch of road (at least 60 m) was subjected to the same lighting level. The experiment ran for eight nights at each site, with the lighting level switching every two nights, i.e. each lighting level ran for two consecutive nights. The lighting schedules were randomized across sites to prevent any order effects, and sites were separated by at least 1 km to ensure the collection of independent samples. The lighting levels we used were representative of differing light intensities being employed by local authorities. Light levels were controlled using pulse width modulation by a sub-contractor of Hertfordshire County Council using a CMS.

All the street lights used in this study were neutral LED lights (MIDI, 97 W, 4250 K, Urbis Schreder, Basingstoke, RG24 8GG, UK) that were 10 m in height. We selected street lights along tree lines that contained trees more than 4 m in height, and each site was at least 20 m from the beginning of the tree line [15,35]. All sites were also close to other linear features such as hedgerows, and typical bat foraging habitats, such as woodland and grassland, were at least 35 m from a building, and were located on A (major) roads in suburban areas that experienced similar traffic intensity. To ensure that lighting levels were comparable across sites, both illuminance (lux) and irradiance ($\mu W\ cm^{-2}\ nm^{-1}$) were measured. We used a TES 1330 lux meter (ATP Instrumentation Ltd, Ashby-de-la-Zouch, LE65 2UU, UK) at 1.8 m from the ground, directly underneath the lantern of the street light to measure illuminance, and a calibrated Ocean Optics USB 2000 spectrometer (Largo, FL 33777, USA), a 7 m P400-3-UV/VIS patch cord and a CC-3 cosine corrector, all positioned 5 m directly underneath the lantern, to measure irradiance. Irradiance readings also allowed us to ensure that the spectral output of the street light remained unchanged and that only intensity varied with each light level (figure 1).

We measured bat activity by monitoring echolocation calls using SM3 bat detectors (Wildlife Acoustics, Inc., Maynard, MA, USA). Three sites ran concurrently. Bat detectors were set to record activity using triggers from 30 min before sunset on the first night until 30 min after sunrise on the ninth morning. At each site, one bat detector was attached to the middle experimental lighting column 1 m below the lantern, using street sign and Jamtorque sign-fixing clamps, with the microphone on the detector pointing slightly downwards and positioned on the same side of the column as the lantern. Bat detectors were randomized across sites. Files were stored as wavefile audio (WAV) files. The settings on the detectors were: high-pass filter 16 kHz; sample frequency 384 kHz; minimum frequency 16 kHz; maximum frequency 120 kHz; maximum recording time 15 s; trigger level 12 dB.

Bat activity for each lighting level was measured as the number of passes over each two-night period. Each 15 s file containing echolocation calls was considered as one bat pass [36]. At sites 19, 20 and 21 the sub-contractor failed to change the lighting level according to the agreed schedule, so bat passes were only counted for one night per treatment, which was selected at random. To compare bat feeding rates at different light levels, we calculated the buzz ratio, i.e. the proportion of passes that contained a feeding buzz [37] at each lighting level.

At seven sites (one from each of the three recording periods), a 12 megapixel 1080 HD Hunting Trail Infra-Red Camera (SpyCameraCCTV, Bristol, BS5 9PQ, UK) was attached to the lighting column to estimate the number of insects attracted to each lighting level. Infrared cameras were used so that the number of insects could be estimated when the street lights were dimmed to low light levels (25%) or switched off (0%). The camera takes high-resolution still images (12 megapixels) meaning that even small flies appeared on the images. The camera was attached to the lighting column immediately below the lantern, so its focus was within the light cone. A burst of three still images were taken once an hour throughout the night (sunset until sunrise). These data were used to compare the attractiveness of the LED lights at different lighting levels to aerial insects.

Nightly temperature and humidity were recorded at each site with a Tinytag TGP-4017 Plus 2 Internal Temperature data logger (Gemini Data Loggers UK Ltd., Chichester, PO19 8LJ, UK). Mean nightly rainfall (mm) and wind speed (km hr^{-1}) were obtained from Met Office weather stations within 35 km of each site (www.metoffice.gov.uk/).

2.2. Data processing

All bat calls were analysed using KALEIDOSCOPE PRO (v. 3.1.1, Wildlife Acoustics, Inc.) with British Bat Classifiers (v. 3.0.0). The auto-identification of *P. pipistrellus* and *P. pygmaeus* was accepted [36]. However, all other calls were manually identified to either species (*Eptesicus serotinus*, *Nyctalus noctula*, *Pipistrellus nathusii* and *Plecotus auritus*) or group (*Myotis* spp.); *Myotis* spp. are usually grouped because of the difficulty of separating the echolocation calls of the different species [38–40]. We also manually identified files that had a margin factor of zero (either KALEIDOSCOPE PRO was unable to identify the call or classified the call as a noise file). Margin scores in KALEIDOSCOPE PRO are uncalibrated confidence scores, whereby higher values are more likely to be correctly identified than lower values. Species identification was verified for 0.5% of the bat echolocation call files (676 files) to ensure that the auto-identification software was working effectively. These files were randomly selected across all sites to account for any differences between sites and included noise files to ensure that all files that contained a bat pass were being included in the analysis.

As we did not manually verify species from every file, we calculated the feeding buzz from a representative sample of files. For each site, we separated calls for each lighting level, then randomly selected 5% of files to check if a feeding buzz was present (mean number of files per lighting level were 35, 44, 51 and 48 for 0%, 25%, 50% and 100% lighting levels, respectively). We identified all feeding buzzes from all species, but they were mostly from *P. pipistrellus*. All noise files were excluded as a bat pass had to occur for a feeding buzz to be present. We calculated the buzz ratio to determine how the proportion of feeding buzzes compared with the number of echolocation calls changed with light intensity.

Insect activity was determined for one night of each lighting level, when there was no rain; this was owing to the difficulty in identifying the presence of an insect from an image when raining. Each visible white dot on the image was counted as an insect [12]. Only insects that were within the light cone, i.e. directly underneath the light were counted and we excluded non-volant invertebrates, i.e. we did not include spiders, many of which make their webs on street lights [41]. It was only possible to estimate total insect abundance and not to identify species. The number of insects counted in each image was carried out blind, i.e. the scorer was unaware of the lighting level when counting the number of insects. The number of insects from the three images for each hour was averaged and the hourly totals then averaged over the night for each lighting level. This reduced 'noise' that might be introduced if any of the three images were unclear.

2.3. Statistical analyses

Data were analysed in R STUDIO using R v. 3.3.3 (R Core Team 2017). We used generalized linear mixed models (GLMMs) to determine potential drivers of bat activity, insect counts and buzz ratios using the lme4 package [42]. Models for bat activity and insect counts followed a negative binomial distribution with a log-link function, and the model for buzz ratio followed a binomial distribution with a logit-link

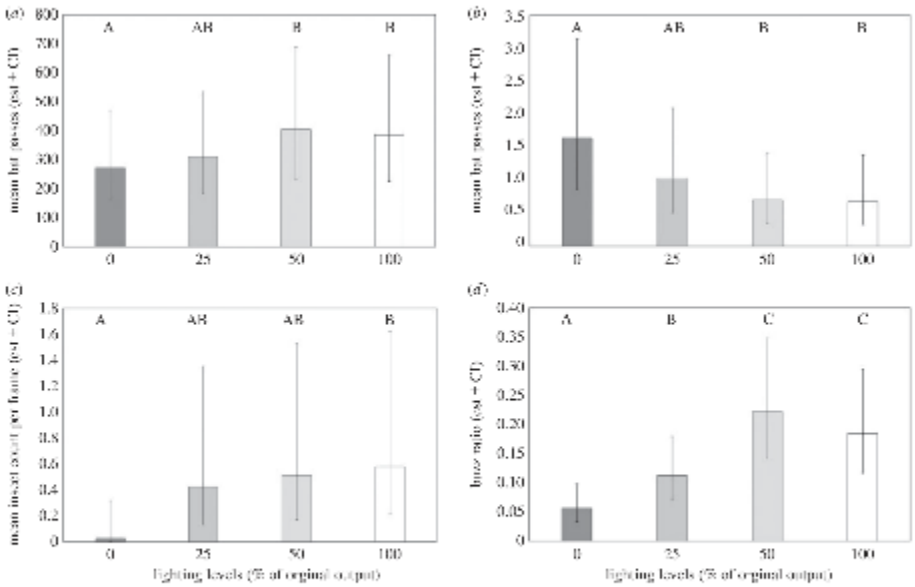

Figure 2. Mean predicted bat activity (number of bat passes) back-transformed across all sites ($n = 21$) for each lighting level for (*a*) *Pipistrellus pipistrellus* and (*b*) *Myotis* spp. (*c*) Mean predicted insect counts back-transformed across selected sites ($n = 7$) for each lighting level. (*d*) Mean predicted buzz ratios back-transformed across all sites ($n = 21$) for each lighting level. For all graphs letters identify groups that were significantly different from each other and vertical lines denote 95% confidence intervals (CIs).

function. Model choice was based on backward selection based on the second-order information criterion (AICc) using the bbmle package [43]. If the ΔAICc was less than 2 between models, we chose the model with the fewest number of parameters [44]. Model fit was validated using the Dharma package [45] to ensure that data were not overdispersed and to provide plots of residuals. Before fitting the GLMMs, we checked to see that the predictors, particularly the weather variables, were not correlated i.e. Spearman's rank correlation coefficient less than 0.5 [46].

For bat activity (bat passes), we used three models; all species, *P. pipistrellus* and *Myotis* spp. For all three models, the fixed factors included lighting level (0%, 25%, 50% and 100%) as well as standardized weather variables (centred around a mean of 0 and a standard deviation of 1), mean nightly temperature (°C), mean nightly wind speed (km hr^{-1}) and mean nightly rainfall (mm). Site was included as a random effect to account for repeated measurements within each lighting column. Date was also included as a random effect to account for recording at multiple sites (three sites concurrently). Post hoc comparisons between intermediate lighting levels (i.e. 25% versus 50%, 25% versus 100% and 50% versus 100%) were carried out using the multcomp package [47] with single-step corrected probabilities.

The coefficient of determination (R^2) was calculated to compare the goodness-of-fit across the models for different bat species [48]. In mixed-effect models, R^2 has two classifications: marginal, which is the proportion of variance in the response variable explained by the fixed effects, and conditional, which is the proportion of variance in the response variable explained by both the fixed and random effects [49]. R^2 values for the buzz ratio model were calculated using the MuMIn package [50], and the R^2 values for the bat activity and insect count models were calculated as proposed by Nakagawa *et al.* [51].

3. Results

Across 21 sites, we recorded 135 228 files that included 74 965 bat passes from seven species/species groups. Most passes (76.7%) were from *P. pipistrellus*, followed by *P. pygmaeus* (20.9%), *N. noctula* (1.9%), *Myotis* spp. (0.2%), *Eptesicus serotinus* (0.08%), *Plecotus auritus* (0.08%) and *P. nathusii* (0.08%) (electronic supplementary material, tables S1–S4). No other species were recorded. From the 676 files that were manually verified, there was 87% agreement between the manual and automatic classifications, with 100% agreement with the automatic classifications of *P. pipistrellus* and *P. pygmaeus*. KALEIDOSCOPE

Table 1. Results from GLMMs for the bat passes of (*a*) all species, (*b*) *Pipistrellus pipistrellus* and (*c*) *Myotis* spp., (*d*) buzz ratios for all species (based on a 5% sample) and (*e*) mean insect counts. (All estimates were compared against the unlit treatment (0%). Significant results are in bold. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.)

model	estimate	s.e.	*Z*-value	*p*-value	marginal R^2	conditional R^2
(*a*) all species					0.183	0.832
25%	0.174	0.164	1.059	0.289		
50%	**0.391**	**0.161**	**2.433**	**0.015***		
100%	0.290	0.160	1.810	0.070		
temperature (°C)	**0.473**	**0.093**	**5.084**	**<0.001*****		
wind speed (km hr^{-1})	**−0.191**	**0.074**	**−2.572**	**0.010****		
(*b*) *P. pipistrellus*					0.203	0.851
25%	0.130	0.169	0.767	0.443		
50%	**0.386**	**0.168**	**2.304**	**0.021***		
100%	**0.343**	**0.167**	**2.054**	**0.040****		
temperature (°C)	**0.531**	**0.097**	**5.452**	**<0.001*****		
wind speed (km hr^{-1})	**−0.252**	**0.079**	**−3.207**	**0.001****		
(*c*) *Myotis* spp.					0.126	0.797
25%	−0.408	0.231	−1.771	0.077		
50%	**−0.828**	**0.237**	**−3.501**	**<0.001*****		
100%	**−0.740**	**0.242**	**−3.057**	**0.002****		
rain (mm)	−0.340	0.184	−1.844	0.065		
wind speed (km hr^{-1})	−0.201	0.111	−1.861	0.063		
(*d*) buzz ratio					0.061	0.196
25%	**0.689**	**0.217**	**3.170**	**0.001****		
50%	**1.371**	**0.218**	**6.292**	**<0.001*****		
100%	**1.190**	**0.220**	**5.406**	**<0.001*****		
temperature (°C)	**0.427**	**0.168**	**2.540**	**0.011***		
(*e*) insect counts					0.188	0.227
25%	2.686	1.422	1.888	0.059		
50%	2.729	1.423	1.917	0.055		
100%	**2.905**	**1.415**	**2.053**	**0.040***		

occasionally classified a file as a noise file or was unable to determine a classification, even when a call was present. As all files that were not classified as *P. pipistrellus* or *P. pygmaeus* were manually identified, we feel that our method was appropriate, given the large amount of data collected and the time needed to analyse all the data manually.

Across the 21 sites, mean light intensities for each lighting level were 11.35 lux (s.d. 3.23, range 8.68–14.9 lux) for 25%, 20.23 lux (s.d. 3.23, range 16.77–23.9 lux) for 50% and 33.46 lux (s.d. 5.94, range 29.4–44.0 lux) for 100%.

Statistical analyses were carried out on the number of bat passes for all species, *P. pipistrellus*, *Myotis* spp., feeding behaviour (buzz ratio) and mean insect counts, with standardized weather variables included as fixed factors in the GLMMs. The best models, determined by the lowest AICc values, generally included temperature (°C) and wind speed (km hr^{-1}) but not mean nightly rainfall (mm). Temperature had a positive significant effect on the number of bat passes, i.e. there were more bat passes as the nightly temperature increased, whereas wind speed had a significant negative effect on the number of bat passes, i.e. there were fewer bat passes as the nightly wind speed increased. So, it was important that both variables were included as fixed effects in the model.

Table 2. Results of the post-hoc comparisons applied to GLMMs for the bat passes of (*a*) all species, (*b*) *Pipistrellus pipistrellus* and (*c*) *Myotis* spp., (*d*) buzz ratios for all species (based on a 5% sample) and (*e*) mean insect counts. (Lighting levels were 25 (25%), 50 (50%) and 100 (100%). Significant results are in bold. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.)

model	estimate	s.e.	*Z*-value	*p*-value
(*a*) all species				
50–25	0.217	0.161	1.343	0.536
100–25	0.116	0.159	0.727	0.886
100–50	−0.101	0.157	−0.641	0.919
(*b*) *P. pipistrellus*				
50–25	0.257	0.167	1.535	0.416
100–25	0.213	0.164	1.298	0.564
100–50	−0.043	0.163	−0.265	0.994
(*c*) *Myotis* spp.				
50–25	−0.420	0.257	−1.635	0.358
100–25	−0.332	0.265	−1.253	0.592
100–50	0.088	0.271	0.325	0.988
(*d*) buzz ratio				
50–25	**0.682**	**0.163**	**4.192**	**<0.001*****
100–25	**0.501**	**0.161**	**3.116**	**0.010****
100–50	0.181	0.161	1.125	0.670
(*e*) insect counts				
50–25	0.043	0.723	0.059	1.000
100–25	0.219	0.696	0.315	0.988
100–50	0.177	0.689	0.257	0.994

When considering all bat species, there were significantly more bat passes at 50% compared to 0% lighting levels, but not between 25% or 100% and 0% levels (table 1). For light-opportunistic *P. pipistrellus*, the results were broadly similar: there were significantly more passes at 50% and 100%, compared with the 0% lighting level, but there was no difference in the number of bat passes between the 0% and 25% lighting levels (table 1 and figure 2*a*). Conversely, higher light intensities had a negative effect on the light-averse *Myotis* spp. There were significantly fewer *Myotis* passes at 50% and 100% lighting levels, compared with the unlit treatment, but there was no significant difference between the 0% and 25% lighting levels (table 1 and figure 2*b*).

The insect count data also showed significantly higher insect activity at the 100% lighting level compared with the unlit treatment, but there was no difference between 0% and 25% or 50% lighting levels (table 1 and figure 2*c*). There were significantly more feeding buzzes at 25%, 50% and 100% lighting levels, compared with the unlit treatment (table 1 and figure 2*d*).

While there were no significant differences between intermediate light levels, i.e. 25% compared to 50% or 100%, or 50% compared to 100% (table 2) for the bat activity data for any of the species or insect counts, there were significantly more feeding buzzes at 50% and 100%, compared with the 25% lighting level (table 2).

4. Discussion

Our results are broadly consistent with our hypotheses, that higher light levels (50% and 100%) increased the activity of light-opportunistic species such as *P. pipistrellus*, but reduced the activity of light-averse species such as *Myotis* spp. However, lower light levels (25%) do not affect activity levels of either light-opportunistic or light-averse species of bats compared to the unlit treatment (0%).

The increase in the number of bat passes of the light-opportunistic *P. pipistrellus* at 50% and 100%, compared to the unlit treatment, is most probably owing to the greater number of insects being attracted to the street lights at higher lighting levels. This supports the attraction-by-insects hypothesis, as opposed to the attraction-by-artificial-light hypothesis, which argues that bats are attracted to the lights for other reasons [14]. Foraging benefits can also be inferred from the buzz ratio data. The proportion of feeding buzzes compared to the number of bat passes was significantly higher at the 25%, 50% and 100% lighting levels than the unlit treatment. Also, there were significantly more buzzes relative to echolocation calls at the 50% and 100% lighting levels compared to the 25% level. Our feeding buzz data suggest that the main benefit for some species of bats flying close to street lights is to prey on the insects attracted to the light source. Even though the number of light-opportunistic bat passes did not increase significantly at the 25% lighting level, compared to the unlit treatment, nor between intermediate lighting levels (i.e. 25% and 50% or 25% and 100%), the buzz ratios increased, suggesting that these species of bats increase their feeding efficiency at street lights. This could be owing to the reduced anti-predator behaviour of moths [52] or because around street lights bats may possibly feed on large numbers of relatively small insects that have a lower energy content than larger insects.

Furthermore, there were significantly more insects at the 100% compared to the unlit treatment and the differences between the 25% and 50% lighting levels and the unlit treatment were almost significant (table 2). While there were not significantly more insects at the 25% or 50% lighting levels compared to the unlit treatment, there were more feeding buzzes relative to the number of bat passes. This could be owing to the absence of a linear relationship between the number of insects attracted to a light source and its illuminance [53]. Although the light intensity at the 50% level (mean 20.23 lux) was double that of the 25% level (mean 11.35 lux), this does not mean that double the number of insects should be attracted to the 50% lighting level. To determine the attractiveness of a light source, it is necessary to consider the spectral sensitivities of the insects [3] and calculate either the square root of the ratio between the illuminance of the light source and its surrounding background [54] or use a function of the luminance of the light source [55]. The difference between the insect and buzz ratio data could also be owing to the smaller sample sizes for the insect counts.

Lighting level appeared to have a stronger effect at 50% than 100% for both bat activity and feeding behaviour, possibly because when the LED street lights are at 50% of their original output, there is an increase in insect numbers and hence feeding opportunities but fewer risks from potential predators. Alternatively, when light intensities increase above 50% of the original output, the illuminance may disturb bats [56] or, at light intensities above 50%, more bats may be attracted to the higher insect numbers, and hence be affected by echolocation interference from the calls of other bats. This makes it more difficult for a bat to differentiate its own returning echoes from those of conspecifics [57].

It is unsurprising that we found significantly fewer bat passes of *Myotis* spp. at 50% and 100% lighting levels compared to the unlit treatment [26,33]. However, it is encouraging that the low lighting level (25%) did not have a detrimental effect on the number of *Myotis* spp. passes. From a conservation perspective, this is a positive outcome as it means there is scope to work with local authorities to determine if it is possible to find a light intensity that is acceptable for humans but does not adversely affect bat activity, particularly for light-averse species.

At the low lighting level (25%), as less light was distributed from the light source, it is likely that dark corridors were created that light-averse species, such as *Myotis* spp., could fly along, either as a more efficient commuting route or even to forage. However, once the street light intensities exceeded 11.35 lux, the perceived threat of predation becomes too great, significantly reducing the number of *Myotis* spp. passes near the street lights. This contrasts with an earlier study, which found that LED light intensities as low as 3.6 lux negatively affected the number of bat passes from light-averse bats such as *Myotis* spp. and *Rhinolophus hipposideros* [26]. This could be owing to differences in experimental design: our study took place in suburban areas, where street lights have existed for decades, and hence the bats may have adapted to the presence of artificial lights, whereas the earlier study set up street lights in unlit areas [26], and hence the novelty of lighting may have affected the bats differently. Differences could also be because fewer *Myotis* spp. are found in suburban areas compared to rural areas (figure 2*a*,*b*). As *Myotis* spp. are light-averse, they tend to avoid suburban areas when commuting and foraging, preferring more cluttered habitats [17,19]. Our results are consistent with an earlier study which also found that light intensity had a significant positive effect on light-opportunistic species such as *P. pipistrellus*, but a significant negative effect on light-averse species such as *Myotis* spp. [33].

Reducing the light intensities of street lights could also benefit invertebrates by decreasing flight-to-light behaviour, thereby lowering the risk of mortality from exhaustion and predation, as well as

preventing disruptions to biological cycles [58,59]. To reduce the ecological impact on invertebrates, it has been advised that LED street lights should be dimmed to 50% of their original output (less than 14 lux) and adhere to a part-night lighting scheme, i.e. switched off between midnight and 04.00 [60].

In conclusion, our results support dimming as an effective strategy to mitigate the ecological impacts of street lights as it seems possible to achieve a light intensity that could benefit both light-opportunistic and light-averse species of bats [56], potentially realigning the balance that existed before street lighting dominated our landscapes. It is worth mentioning that ideally the installation of street lights should be avoided, but as this is not feasible in many areas owing to safety and security reasons, dimming seems to be the most suitable alternative.

We believe further studies are required to investigate the impacts of dimming in different locations to include other light-averse species, such as *Plecotus* and *Rhinolophus* species. It would also be useful to repeat this study, using residential areas, instead of A roads where street lights are typically 5 m as opposed to 10 m high, and have a lower power and illuminance. It might be possible to reduce light intensities even further, while still striking the balance between maintaining biodiversity, economic benefits and human safety [61].

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. Conceived and designed the experiments: E.G.R., S.H. and G.J. Performed the experiments and analysed the data: E.G.R. Contributed reagents/materials/analysis tools: E.G.R. and G.J. Wrote the paper: E.G.R., S.H. and G.J. Supervised the study: S.H. and G.J.

Competing interests. We declare that we have no competing interests.

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